THE BEHAVIORAL ECOLOGY AND BREEDING BIOLOGY OF THE ANDEAN SPARROW, *ZONOTRICHIA CAPENSIS*

By

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(A contribution from the Museum of Vertebrate Zoology
of the University of California)

RESUMEN:

La ecología de comportamiento y la biología de la reproducción de los Gorriones Andinos "copetones" *(Zonotrichia capensis)* fueron estudiadas a lo largo de un año en una población ubicada a 2.000 metros de altura en la Cordillera Occidental de Colombia. Se capturaron cerca de 170 individuos, y para hacer posible su identificación en el campo se marcaron convenientemente. En varias ocasiones se logró la recaptura de muchos de éstos con el objeto de estudiar los cambios de plumaje y ciclos reproductivos a lo largo del año. La condición reproductiva de muchos individuos fue evaluada gracias a repetidas laparotomías. Se describen nueve tipos diferentes de vocalizaciones y se discute sus funciones. Se establece la existencia de comunicación entre estas aves por medio de variación del plumaje, posturas y movimientos.

Sólo las hembras construyen nidos, los cuales se colocan ya sea en el suelo o sobre arbustos, pero en ningún caso a más de un metro de altura sobre el suelo. La puesta usual es de dos huevos en dos días consecutivos y en las primeras horas de la mañana. La hembra efectúa la incubación que dura de once a doce días. Los polluelos están listos a abandonar el

* Deceased, October 9, 1965.

nido en 10 o 12 días más. Los machos y hembras jóvenes alcanzan madurez reproductiva entre los 12 y 11 meses de edad. Muchas hembras vuelven a anidar si han perdido el nido con huevos o los polluelos tiernos. Algunas hembras anidan por segunda vez inmediatamente después de haber criado polluelos.

Los machos se establecen en territorios claramente definidos y los mantienen a través de nidadas sucesivas. Los lazos de unión entre los miembros de una pareja duran de una nidada a la siguiente, aun a través de períodos sin reproducción. Los territorios observados tenían típicamente cerca de 30 x 20 metros. La mayor parte de la alimentación parecía provenir del área definida, aunque ocasionalmente pueden abandonarla. Alguna vez una pareja fue vista a 150 metros de su territorio.

Del total de "copetones" adultos establecidos en territorios delimitados a comienzos del estudio, sólo un 71% logró sobrevivir todo el año. Un 13% de los jóvenes sin territorio pudo ser contado al fin del año. Los vacíos que aparecieron en el grupo local de adultos se llenaron con jóvenes, y cerca de la mitad de éstos provenía de áreas cercanas. Rara vez consiguen los padres criar más de un polluelo por nido. Dos y probablemente hasta tres jóvenes pueden ser alimentados fácilmente en el nido mientras permanecen en él, pero depredaciones o alguna otra limitación en el cuidado paternal (y no deficiencia en la alimentación proporcionada en la etapa post-nidal) parecen ser los principales factores negativos respecto a una mayor producción de individuos. El régimen climático y la falta de estaciones favorecen la nidificación en cualquier época del año; por lo tanto, la ventaja selectiva para la especie consiste en la capacidad de efectuar muchas nidadas y no en la puesta de más huevos por nido.

INTRODUCTION

At middle and upper elevations in Central America and northern South America and in all of temperate South America, *Zonotrichia capensis* is a common emberizine sparrow inhabiting unforested areas where scattered brush cover and grass prevail. It has an ecologic role like that of the four North American species of *Zonotrichia*, but unlike them it seems to have no partial competitors among other sparrows in exploiting these environments over most of its range.

The purpose of this report is to make available data on the natural history and breeding biology of this prominent and ecologically important southern zonotrichia. It is a type of bird known to many naturalists but one whose behavior and ecology has not received concerted attention to the point of being reported in the literature. Interest in it derives from two further considerations. First, as the southern counterpart of the well-studied northern species of the genus, the comparative aspects of its biology deserve attention. Second, some of its races occupy equatorial latitudes where seasonal events are of a very different kind and order of magnitude from those influencing the biology of other races and species of *Zonotrichia* which are occupants of temperate parts of the Americas.

Zonotrichia capensis is known variously as the Andean sparrow and the rufous-collared sparrow, terms descriptive of features of its range and appearance, and in some parts of the Spanish speaking areas it is known as copetón in appropriate reference to its pointed crest, which among other features distinguishes it in life from its northern-relatives. As Chapman's (1940) taxonomic review of the species brought out, its very large range extends from the mountains of Chiapas and the Dominican Republic south to Tierra del Fuego. In the tropical latitudes it occurs locally and irregularly near sea level as on the islands of Curaçao and Aruba, in French Guiana, and at the mouth of the Amazon. But the great part of its range and that in which it has its greatest success is in the Andean mountain system and generally in subtropical and temperate climates. The dense populations which the species often develops and its capacity to colonize new areas mark it as an ecologically dominant and aggressive type. For example, it has extended downward from the mountains into very hot arid interior scrub land in tropical Colombia, as at

2500 feet in the Patía Valley, and it has invaded towns and cities as a street sparrow taking part of the role that one sees in *Passer domesticus* of the northern continents. It is indeed a weed-like species, thriving in disturbed habitats where forests have been cleared.

As a species of the great range indicated, and one which is largely resident and in places locally isolated, *capensis* has evolved into many races. Chapman (1940) recognizes 22, and clearly many adaptive features of color and structure as well as physiology are involved. Chapman's contention that these races are the consequence of a geologically recent invasion of South America because many of them are not strongly marked is not convincing. This is especially so since the racial differentiation in even shorter time by *Passer domesticus* in a century of new occupancy of North America has produced quite as distinct evolutionary changes (Johnston and Selander, 1964). In other words rates of evolution cannot be judged with any great accuracy from inspection of differentiation at one time level alone. Moreover, assumptions made from that basis cannot provide any convincing arguments for the time of invasion as Chapman did. Chapman's highly speculative "post-glacial history" of *Zonotrichia capensis*, although having some elements of probability, must not be taken as resting on any real facts. It assumes that the species or its ancestors arose in the north, that glacial climatic conditions forced it or permitted it to invade southward in the Pleistocene, and that its level of racial differentiation reflects a geological recent invasion. Alternative possibilities simply cannot be ruled out. New evidence and a much more through biosystematic analysis is needed to throw more light on these questions. Such an attempt is not the function of this report and we are convinced that no one possesses adequate data at this time to undertake it.

Concerning the classification of *capensis* as a species of *Zonotrichia*, the question about this was answered satisfactorily long ago by van Rossem (1929) and confirmed by Chapman (1940). Nothing in what we are able to report of its biology indicates otherwise. Indeed all new evidence supports the view that it is a *Zonotrichia* in the restricted sense and that other closely related sparrows like *Melospiza* and *Junco* are less closely allied. It is not appropriate here to go into questions of morphologic evidence for generic affinities and groupings, but a careful inspection of skulls of species of *Zonotrichia*, *Melospiza*, *Passerella*, and *Junco* that the senior author has made shows very close resemblance of *capensis* to *Zonotrichia (sensu stricto)* and particularly to *albicollis* in the matter of squamosal inflation, somewhat in disagreement with Tordoff (1954). Moreover, details of the junction and shape of the squamosal border and the zygomatic process above the auditory meatus differ in *Zonotrichia*, *Junco*, *Melospiza*, and *Passerella*, and *capensis* fits very closely in this

respect with the other zonotrichias, particularly *albicollis*. These matters of structure need more attention and appraisal before proceeding to regrouping or combining of genera as Paynter (1964) has recently done largely on the basis of external features and some fragmentary evidence on notes and on interbreeding.

The particular population with which this study is concerned is one in the Western Andes of Colombia near the equator (3 ½°N). The birds belong to the subspecies *Zonotrichia capensis costaricensis* which is a resident, short-winged form occurring in the mountains of Costa Rica and western Panamá, Colombia, western Venezuela, and Ecuador. There may indeed be differences of a physiologic nature between some of the populations of this race and there are some minor morphologic divergences (Chapman, 1940). Nevertheless, this population is thought to be representative in general biologic attributes of this equatorial race, even though study of it may not show all the ecologic responses of which the race is capable at different geographic localities within its range.

The equatorial form of *capensis* in the western Andes breeds throughout the year. Each individual shows its own cycles, two periods of sexual competence or activity occurring each year arising out of an innate rhythmic factor. The cycles of individuals are imperfectly coordinated, but the actual nesting, the culminative phase of breeding, shows peak periods correlated with the double wet and dry cycle (Miller, 1959, 1962). The investigation of the breeding cycles was our primary concern during a year spent in residence in the western Andes, but related to it was an understanding of the general behavior and ecology of the species which we gained and which is now presented.

STUDY AREA

The principal locality where we studied *Zonotrichia capensis* is situated on the divide of the Western Andes, at 6500 feet, on the road from Cali to Buenaventura, Colombia. It has been described and in part figured in an earlier report (Miller, 1963), and climatic conditions have been reported. It is, in brief, an area originally of cloud forest, with almost nightly fog and cloud cover and with an annual rainfall of about 53 inches. The temperatures are moderate and insignificantly variable. Daily minima ranged only between 54° and 60°F and maxima between 62° and 78°F for the whole year.

The zonotrichias lived in the cleared pasture lots and forest shrub borders and about the gardens of the numerous country homes of the

area. Large, heavily grazed pastures with few or no bushes or low trees were avoided by the sparrows and the birds never penetrated the forest beyond the edge of the second growth. Invariable the grass and bushes were at least somewhat wet in the morning, even in the dry season. Torrential rains seldom lasted more than an hour at such intensity as to drive the birds to cover.

We concentrated our efforts in 1958 and early 1959 close about the house known as Santo Domingo (pl. 3, a) and its walled and fenced gardens, chiefly within a radius of 500 feet; territories of twelve well studied pairs (see p. 130) fell within a radius of 200 feet. In March of 1965 we studied the species at a point 4 kilometers to the northwest at the same elevation (pl. 3, b).

PROCEDURE

The local population of sparrows was banded as rapidly as possible following our arrival at the station on February 9, 1958. Each bird received an aluminum numbered band and a distinctive color band combination. Birds were captured by use of Bailey traps (Bailey, 1951), occasionally supplemented by netting. By the end of the first month 65 birds had been trapped and marked. In the course of the whole year 170 individuals were thus marked, the later ones being largely juveniles and immatures produced in the course of the year.

Retrapping of the birds through the year to gain information on age, molt, and breeding state by external evidence and laparotomy was not disruptive of normal behavior. No loss from laparotomy occurred and birds were returned to the field in an hour or less recovered from anesthesia. They at once resumed normal behavior in relation to their mates and neighbords.

Observations of activities and trapping of sparrows were recorded on 234 days through the year 1958-1959, most of the data being derived from individually identifiable birds. Some observations were made connected with collecting of 81 sparrows for tissue samples at points ½ mile or more away from the marked population. Work at Santo Domingo was interrupted occasionally by short trips away, the longest of which was 22 days in August. Observations stopped with our departure from the station on January 23, 1959. All statements relate to wild birds unless otherwise specified.

A small captive colony was maintained for experimentation, observation, and breeding at Berkeley, California, beginning in 1959. This was greatly augmented by birds captured by us in 1965.

The authors shared field activities in trapping, netting, marking, and examining birds and in observing at sparrow nests during the incubation and nestling periods.

Acknowledgements

The study of Andean sparrows in Colombia was made possible through the support of a Guggenheim Fellowship and through sabbatical leave privileges in 1958 and 1965. F. Carlos Lehmann V. aided in innumerable ways essential to the conduct of our field work in Colombia and the Universidad del Valle in Cali, through several members of its faculty, assisted, as did the Museo Departamental de Historia Natural in Cali in 1965. Indeed the invariable courtesy and interest of Colombians whom we met while conducting the research contributed greatly to the undertaking. In 1958 our daughters Barbara and Patricia assisted substantially with the study of the population of sparrows at our station at Santo Domingo.

The facilities of the University of California Behavior Station at Berkeley made possible the maintenance of captive birds and observation of their behavior and reproduction; this facility was provided through grant G-13526 of the National Science Foundation. Maintenance of the colony and of records on it was supported by grants from the Committee on Research of the University of California. Two assistants, Hans J. Peeters and Larry L. Wolf, contributed particularly to the study of the behavior of captives. Gene M. Christman is largely responsible for the figures and for the photographs of captive birds.

COMMUNICATION

Voice

The vocal communications of *Zonotrichia capensis* are in general similar and homologous with those of *Zonotrichia leucophrys* and *Zonotrichia atricapilla.* Less perfect parallels are found in the notes of *Melospiza (Passerella) melodia* and *Passerella iliaca* and of species of *Junco.* The general character of these communications and the context in which they are used are as follows:

Anxiety.—A *chip* or *chunk,* loud and sharp, as in all four other species of *Zonotrichia.* Even though this is a short note (fig. 1), it has a downward slur and a slightly broken or bleating effect, at once distinguishable by this from the *chink* notes of *leucophrys* and *atricapilla.*

The note is given when the bird is alarmed, disturbed, or generally

anxious and alert to danger. Because of its carrying powers, it also serves, perhaps only incidentally or secondarily, as a location or station note. The note is given when nests or young are endangered, sometimes when the bird is flushed or when pursued by other sparrows, and usually it is heard at dusk as the bird settles for the night and sometimes at first arousing in the morning. The evening use is particularly like that in *leucophrys* and *atricapilla.*

Alarm.—A high-pitched *tst* of limited carrying power and slight volume. This is homologous to notes in other emberizine sparrows given under similar circumstances.

In *capensis* the note was heard only when we were at a nest or near recently fledged young. The parents will shift from the loud anxiety note to this alarm note when on guard at a nest. It would appear that it is given when the adult is close to the source of danger and very much on the defensive, perhaps itself ready to flee. At close range when we were at nests in cages this note rather than the anxiety note was given. Yet once when a young bird in hand screeched in fear, a parent shifted from the high-pitched alarm note to a rapid utterance of the anxiety note.

Defense screech.—A harsh, loud screech or snarl prolonged or repeated variously as the situation demands. (Fig. 1).

This note is given when young or old are physically attacked or when another sparrow is about to make contact with it. We are not sure that we can distinguish different forms of it given by juveniles, females warding off a male attempting to mount, and males in the course of fighting or challenging. It reflects extreme fright and warning under conditions of struggle and desperation. As in many such loud fear notes, it seems to be able at times successfully to distract a predator or combatant. The note is often heard in handling birds of all ages in traps or nets; well-developed nestlings may give it as they are lifted out of the nest. An adult screeched as a smooth-billed ani *(Crotophaga ani)* closed in to attack it as it hung in a net. A female may give this note as a male swoops after her as she leaves the nest, or as she is crowded by a posturing male when she is not receptive to mounting. A female we have held captive with a male *Zonotrichia leucophrys* is repeatedly approached by the displaying male who often grasps rump or tail feathers in futile or uncoordinated efforts at copulation (only occasional infertile eggs resulted); the *capensis* then screeches repeatedly until his pursuit stops. In the instances of males giving it as they make or approach contact we have not always been able to tell whether it is the aggressor or the subordinate or fleeing individual that gives it; we suspect it is chiefly the latter, but on some occasions both screech.

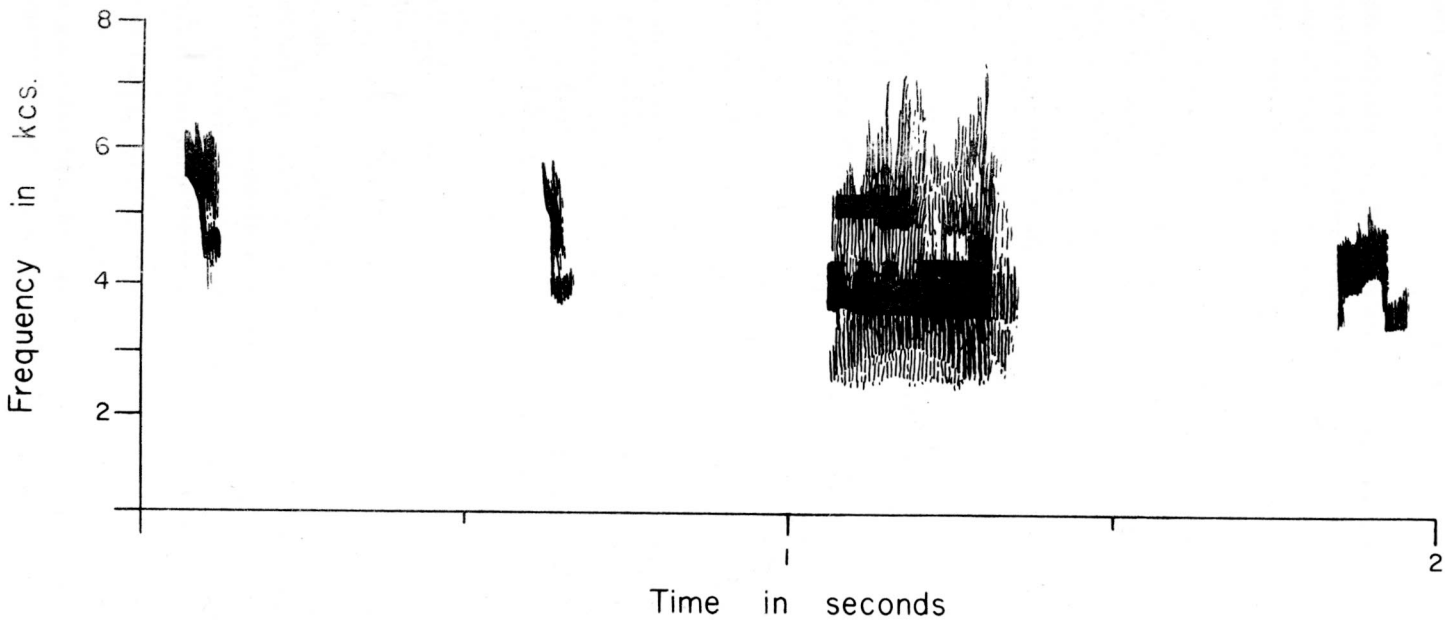


Fig. 1. Sonagrams of notes of *Zonotrichia capensis*. Frequency in kilocycles on ordinate, time in seconds on abscissa. At left are two of the anxiety *chips*, showing the typical downward slur resulting from reduction in frequency. Following, at the center, is a defense screech, showing wide band of principal frequencies in this harsh note; a repetition or pulsing sequence of such a single screech unit often is heard. At far right is the lisping pair association note; it is much fainter than the preceding notes, although this is not reflected in the sonagram drawings.

Song alert.—This is an obvious modification of the normal song described beyond and consists of prefacing a normal song by two or three extra, clear notes. We are not aware of a comparable song modification and use in related sparrows, although occasional use of unmodified song under stress or anxiety is known (see Blanchard, 1941: 21).

In *capensis* the senior author began to associate this special song with his intrusion on the song post area of certain males and on other occasions with hawks passing overhead. The song is given just once and is quite independent of normal song bouts that may have preceded or succeeded it at short intervals. One captive male in a caged flock gives this as we enter the cage. The most clearcut performance of this special song which revealed to us its distinctiveness and meaning occurred on July 27. A hawk, *Buteo magnirostris*, was flying toward the finca from the southeast. As it crossed the territory of male 475, he gave the special song, followed by a similar song from male 460 and one from male 468 on adjacent territories as the hawk passed successively over them. Later, on hearing this song, we were able on several occasions to look quickly and catch a glimpse of a hawk overhead.

Pair association.—A faint lisping *sep*, short and downwardly inflected, and not at all harsh or sharp (fig. 1). It is usually audible no more than 25 feet away.

This note was detected only when two sparrows were foraging on the ground or moving about in the bushes together, usually within 20 feet. There were no associated aggressive moves and indeed only obvious quiet awareness of one another. These circumstances make it highly likely that the note serves to keep members of a pair in touch and it may be an actual pair attraction or pair-bonding note. Possibly it is given between birds which are not members of a pair at group feeding areas but we could not be sure of it in this context in the field. It is heard in the flock groups in the aviaries. The note is the homolog of what Blanchard characterizes as *eep* in *Zonotrichia leucophrys*, but it is fainter and shorter.

Nestling begging.—A faint *see* is audible in nestlings from the age of about 4 days on. This has been heard in captives as they gape for food. It is significant that this note is not audible at a distance of more than a few feet up until the time of departure of the young. Thus there is no sound likely to attract a predator to the nest from any significant distance.

Fledgling note.—A rough *chir* or *chip*, not a sharp or abrupt as the anxiety note of the adult although resembling it.

This note is given just before or beginning with and following nest departure. It serves as a location note and a hungry juvenile gives it

continually. As food is brought to it or when the young one is close to an adult, the note changes over into a wheezing call, wheedling and vibrant, as food is actually thrust into the mouth; this may be heard readily at distances of 50 feet.

Pre-copulatory warble.—This consists of a trill or warble, not clear but rather reedy, and of slight volume; it almost suggests a juvenile's subsong. It is a less simple trill than in *Zonotrichia leucophrys.*

This note was given by females at the time of nest building and egg laying and it was associated either with postures inviting copulation or the presence of the male nearby. This was given at least three times in the course of the morning of November 30 by female 385; on this date she had a completed nest and on December 3 the nest held one egg. No special note is given by the male in the nest building or laying period such as occurs in *Zonotrichia leucophrys* according to Blanchard (1941: 22).

Song.—The song is a series of three to five notes in which there is a dominant accented or prolonged note with a downward inflection in the mid-section of the sequence. No one of these notes is conspicuously buzzy but a short terminal trill may or may not be added (fig. 2). The inconspicuousness of the trill and the general downward inflection of the clear notes in the song contrast with the songs of *Zonotrichia leucophrys* (fig. 2). The overall resemblance of the songs of the two species is evident but we have never heard songs that one would misidentify as to species. This is true despite the considerable differences in song dialect in *leucophrys* (see Marler and Tamura, 1962) and the apparent but as yet undocumented dialect types in *capensis.*

The songs from the San Antonio area usually were of a pattern closely similar to those recorded in two captive males from the population of that locality. One individual may have two to four slightly different song patterns but this is not usual, nor does one hear a male with alternate patterns shift frequently from one to another. Male 480 had an unusual shortened song with just two notes, the counterpart of the opening notes of a normal song.

The young males brought from Colombia in 1959 had begun singing there in outdoor cages with wild males audible all about them, and in Berkeley they have persisted in these same songs without detectable modification while will *Zonotrichia leucophrys* sing in the vicinity or in adjoining cages.

The juvenal male begins giving a subsong in captivity at an age of 35 days. At 4 ½ months of age in young males artificially stimulated by long photoperiods a definitive adult-type song was given regularly. Such

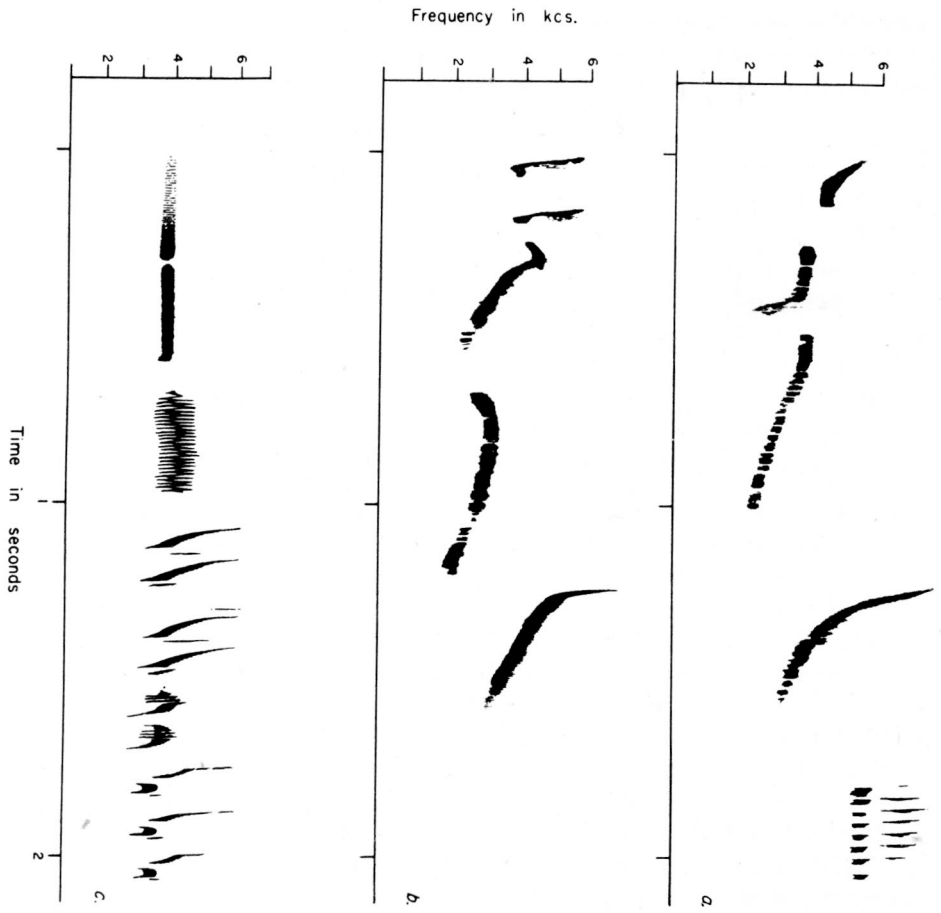


Fig. 2. *a, b.* Sonagrams of songs of two males hatched in Colombia en 1958 but maintained as adults for many years in adjacent cages in Berkeley. The contrast in the pattern is representative of individual differences in songs of wild birds. The song of male was itself varied at times by the omission of the terminal trill. Many songs of the species lack even this short trill. *c.* Sonagram of representative songs of *Zonotrichia leucophrys* adapted for comparison from figure 2M of Marler and Tamura (1962). In contrast to *Zonotrichia capensis,* note the lack of the downward slur of introductory phrase, the presence of a more vibrant middle syllable, and a longer terminal trill, which is consistently present though variable in form.

does not appear in the wild until 5 or 6 months of age when young males normally reach breeding condition.

We have one record of a captive female singing during a period when she was not receptive to the advances of the male in her own cage but was trying to get at a male of a pair visible in an adjoining cage. Her song was subdued and somewhat rapid compared with that of males. Despite this occurence, we believe that female singing is abnormal. Perhaps it is stimulated by special or unusual pair relationships as Blanchard (1936: 149) reported in the case of a polygynous situation in *Zonotrichia leucophrys*. We never detected song in the field among our color-banded females.

Song is delivered by the males almost entirely from a series of habitually occupied song posts in their territories. Usually the birds are in full view on a bush top or on an exposed limb beneath a higher canopy. Heights of posts varied from one foot to 30 feet but most were in the range from 3 to 20 feet. Occasionally we heard songs as a male hopped along the ground and in one instance at least a song was given on the wing between bushes 50 feet apart. A song in full darkness occasionally is heard.

Song is obviously a territorial performance expressing aggressiveness and dominance in the occupied area. The males are conspicuous in this performance and are responsive to the territorial singing of other males. Thus one male that initiates a song period will often be followed in quick succession by song bouts by males on adjacent territories or in adjacent cages. However, fighting at territorial boundaries is rarely accompanied by song nor necessarily preceded by it. Upon return home from such a boundary dispute, song often ensues. In no instance did we hear song from a male delivered inside an area known to be that held by another male.

Song is especially abundant in unpaired males and in males in newly established areas to which females later come (see p. 126). Following pairing it often slackens. In non-breeding periods of a pair, it usually is infrequent, but it is abundant again during courtship, nest building, and at the time when the female is on the nest incubating. In captivity a male usually rushes toward the female as she leaves the nest from an incubating session and sings ecstatically with wings drooped. He then usually stops singing and moves about with her giving the pair association notes. The song thus clearly functions in attracting or signaling a female to an area and in expressing male aggressiveness and mating capacity in the breeding period (diurnal, seasonal and other variable aspects of song frequency are treated on p. 136).

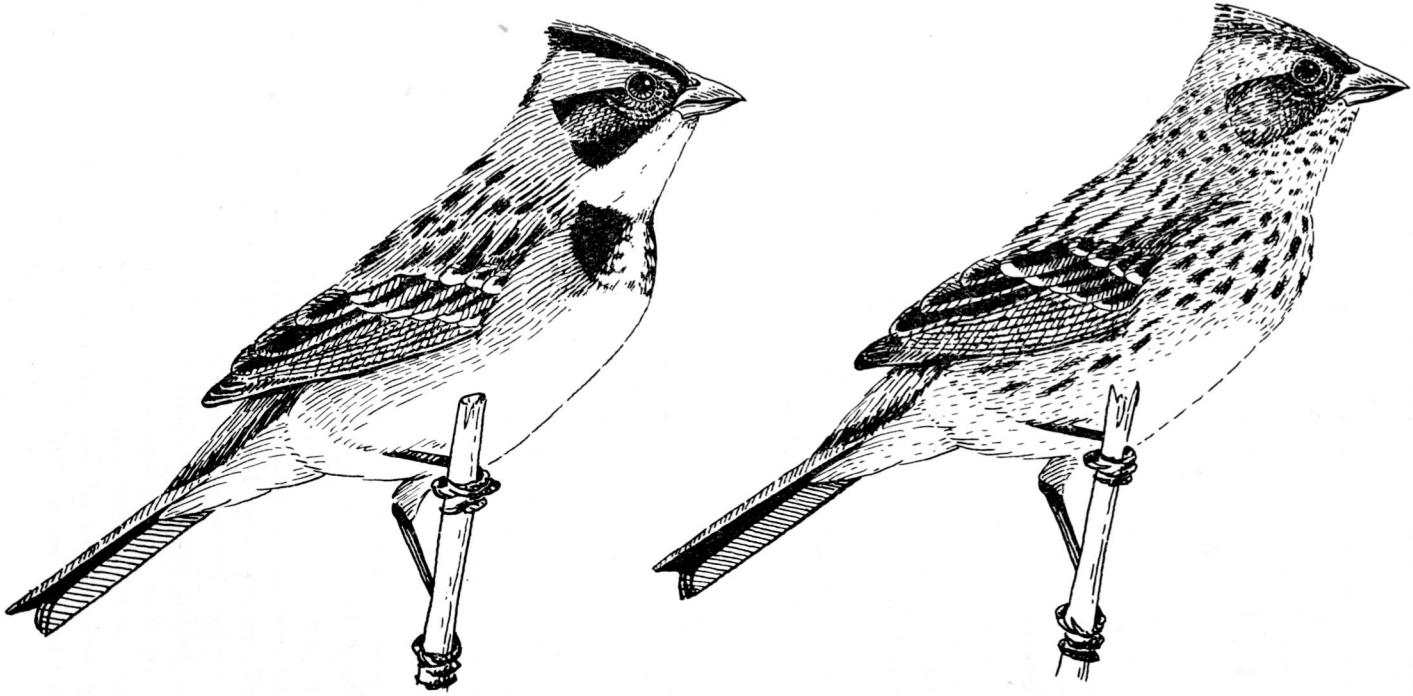


Fig. 3. Contrast in pattern of adult (left) and juvenal plumages of *Zonotrichia capensis*.
Drawing by Gene M. Christman.

VISUAL SIGNALS

Appearance, postures, and certain normal movements serve to communicate information to other members of the species, either simple species identity or special status and attitude.

Plumage.—In the range of *Zonotrichia capensis* in northern South America no other bird of the same size has similar patterning of the head and throat. The distinct head stripes, the chestnut collar areas, and the black throat patches (fig. 3, pls. 1, 2) set it off clearly and must readily communicate species identity to others of its kind, as do also probably much or all the repertoire of notes.

The differentiation of male and female is incomplete. The most sharply contrasting head stripes and richest chestnut color are to be found in males, but neither with live birds in hand nor in study skins can we make a dependable separation and presumably the partial differentiation of color and pattern alone does not reliably communicate sexual status to another zonotrichias. Smaller average size of the female seen in tail length, bill, and general stature may add further cues that with plumage begin to form a total picture indicative of sex, but even here we suspect that behavioral features are necessary for really dependable sex recognition. In a breeding male, at close range in a trap or cage and occasionally in the field we can detect the protruding tuft of anal feathers that result from the enlarged cloacal protuberance. Local native boys using some combination of features from among the foregoing usually could predict the sex.

The juvenal plumage with poorly developed head stripes and finely streaked throat and under parts (fig. 3), as in many young sparrows, differentiates this age and must communicate status. It probably results in an acceptance by established adults of a juvenal-plumaged bird in areas otherwise defended or dominated by them. There is no special subadult or immature plumage intervening between the juvenal and adult types.

Postures.—Crest position. The long crown feathers of this species can either be elevated to a distinct crest (pl. 1, *a*) or completely depressed. Head shape is thus varied from sharply pointed above, to obtusely angled, or to fully rounded (pl. 1, *b*). Even in juveniles the partly elongate crown feathers of this plumage can be elevated sufficiently to produce a noticeable crest.

The crest is lowered when a bird is being closely pressed and is frightened and obviously seeking to escape. In song performances it is sometimes elevated, but not always. In general it is more elevated and

more conspicuous in males. Without an elaborate, quantified record of its display and degree of elevation, we cannot safely further conclude about its correlation with other behavior and about its function. Probably, as Brown (1964) has shown in crested jays, there is elevation of it in aggressive situations, or by a dominant bird, and during periods of alertness and some uneasiness.

Strutting. This consists of drooping the wings and fanning the tail while moderately depressing it. The bird stands fairly high on its legs, especially if on the ground. This action is seen only in males and is of varying intensity. The wings often are drooped a little while singing, but the primaries are drooped further and the tail spread especially as the male approaches the female in courtship.

Coitional invitation. The female invitation is like that in other related sparrows. It consists of crouching, wing fluttering, and elevation of the tail.

Injury feigning. This was seen only once in the field when one of us handled a screeching juvenile that had only recently left the nest. The female came within 10 feet on an open road surface and danced back and forth there with wings spread and fluttering. Such actions were not seen in the field as females flushed from the nest. Then they either flew off or ran or hopped off inconspicuously through the grass and bushes, sometimes hiding in the bushes near the nest. In captivity a female once fluttered within a foot of us near a nest.

Crouching. This is a horizontal posture, the bird crouching down with neck shortened. A bird does this when afraid or subdued in an encounter with another individual. It is the opposite of the rather erect elongated position of an aggressive, alert bird in which the head pattern is differently displayed or emphasized.

Threat. The posture immediately preceding fighting is one of partial crouching but with head thrust forward, in preparation for a jab with the bill (pl. 2, *b*); the back is somewhat hunched or elevated. At slightly greater distances from the antagonist, an erect pose or strutting would precede this close threat.

Flight. This race of *Zonotrichia capensis*, at least, has rather heavy wing loading. Flight is often somewhat labored and driving, without undulations. Nevertheless escape by flight is typically upward into low trees or bush tops not down into tangles as in *Zonotrichia leucophrys*, *Z. albicollis*, or the species of *Passerella*. In this they are more like *Junco oreganus* or *Junco phaeonotus*, even though much less light on the wing. A laying female or a bird in heavy wing molt seems unable to fly above a horizontal course.

Hopping. Progression on the ground is by hopping, not walking. The

hopping may often involve placing one foot somewhat ahead of the other. There is never a deliberate striding and tail swaying as seen in many other grass-foraging species and in *Junco phaeonotus*.

Scratching. Kick-scratching to expose food and spread ground litter is not vigorous or frequent. In the grass of pastures it would have little purpose. Some individuals use it regularly but not persistently in a feeding tray or in leaf litter placed in a cage, scattering seeds and debris with a backward stroke of the two feet simultaneously in a kick-hop action. This may attract another individual to the spot to do likewise.

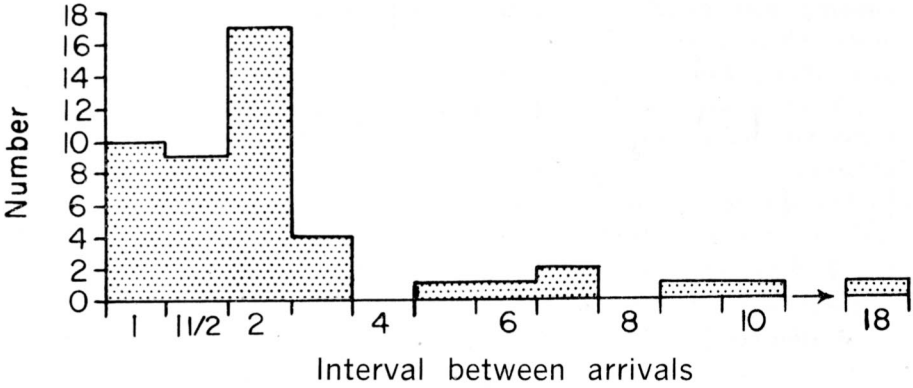
Nesting

Nest Building

The nest is constructed only by the female although males in captivity have been seen carrying material but not placing it. Prior to construction the members of the pair spend much time foraging together and moving about through grass and bushes, the male being more in evidence in this in some pairs than in others. Probably selection of a nest sight occurs in this period, but no specific action related thereto could be discerned, and the location may be determined solely by the female.

The most satisfactory opportunity to watch nest building was afforded by female 485 beginning on December 6. Two days before, this female's nest with fresh eggs had been robbed. The new nest construction thus was a replacement and was probably initiated on the 6th although what actions may have taken place on the 5th we do not know. On the 6th the nest was not inspected at close range, for we wished to avoid disruption of the continuous attention the female was giving it. The nest was 40 feet away from the destroyed nest in the same row of hydrangea plants and about 30 inches above ground.

Construction at this stage was rapid. The replacement nests generally are more rapidly built than first nests of a breeding period. Female 485 was watched continually from a distance of 50 feet for 113 minutes beginning at 8:22 a.m. when she was discovered carrying material. Figure 4 shows the times of arrival at the nest with material. There were 48 deliveries. The intervals between arrivals averaged 2 7/10 minutes, but inspection of the record indicates bursts of intense activity with inactive or rest periods between. During the intensely active periods, intervals between arrivals were almost always 1 to 2 minutes. There was no intervening feeding, preening, or loafing, the female flying to the ground from the nest and immediately gathering the succeeding load. The longer intervals entailed some moving about and at least during the longest one of 18 minutes she went out of sight to a favored foraging area.



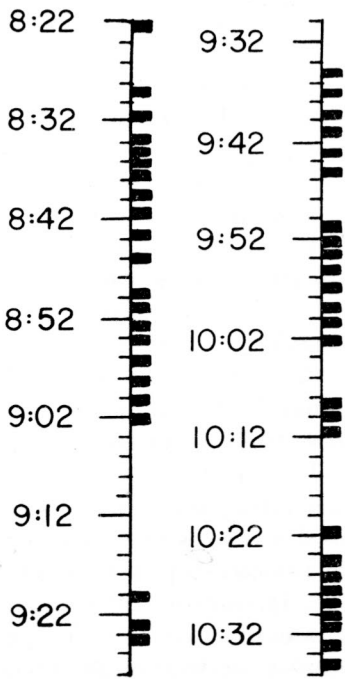


Fig. 4. Nest building activity of female 485 on morning of December 6, 1958. Black bars on time scale indicate arrivals at nest with building material.

The period at the nest used in arranging materials was not always timed and was recorded usually only in ½ minute units. On 24 occasions ½ minute was used. A full minute was involved on 11 occasions. There was one instance of a brief stay of ¼ minute and one case of 1½ minutes, the longest recorded. Therefore during the bursts of intensive building ½ minute of the 1-to-2 minute interval between arrivals was used at the nest, leaving ½ to 1½ minutes for gathering.

The number of pieces of grass or leaves and petioles brought at a time was small, usually 2 to 5 but they were often long, trailing a foot behind the bird as she flew. In two instances the load consisted of an estimated 8 and 10 pieces and the longest arranging period at the nest entailed the arrangement of one of these larger loads. If the average load consisted of about 4 pieces, this female must have placed approximately 200 pieces in the period of a little over 2 hours. This was obviously the coarser basic material of the nest cup. On several occasions we could see her pick up grass and fine twigs or petioles from the ground as rapidly as she would have picked at grain. On another occasion she tugged at soft tangles of compost in the garden and dark, moist leaf or stem fragments were brought, after which she usually wiped her bill on leaving the nest.

This female was obviously not disturbed by us and was not secretive in going to the nest. Indeed at times she came in on direct flight, crashing in among the hydrangea leaves at the nest fork in an awkward and conspicuous way. Other individual females we are sure build less conspicuously, as we have often failed to be able successfully to follow one to a nest site as it moved with material in its bill.

Female 485 obtained all material from the ground in the open in the adjoining vegetable garden, path edges, or cultivated cane-grass slope. She moved in all directions from the nest except downslope and most material was obtained within 6 to 20 feet of the nest. Rarely she moved 40 feet away and several times she obtained material on the ground under or at the edge of the nest bush.

Nest construction ceased at least during part of the day. A watch of one-half hour from 3:46 to 4:16 p.m. revealed no building although the female was in the area.

On the next day a ten-minute watch starting at 8:17 a.m. recorded 4 trips in with material. The vegetable material brought was finer than that of the preceding day, but it was not the type used for lining.

On December 8, the third day of building, watch was kept from 8:37 to 9:07 a.m. during fog which finally turned to rain. In the half hour three trips with lining material were made. At 4 p.m. that day the nest was examined and it appeared finished with the usual fine-grass lining. No further additions of consequence were made and on December 11 the

first egg was laid. Nest construction was therefore accomplished in 3 days and the first egg deposited 3 days after completion, 8 days following the laying of the first egg of the preceding clutch, and 7 days after the loss of that clutch.

The behavior of the mate of 485 during nest building must be judged against his general history of secretiveness and lack of participation in the feeding of young. He (no. 466) was also a male that sang rather little through the year. Other males may be much more in evidence during nest building as fragmentary observations in other territories suggest.

Male 466 sang occasionally during the intensive building on December 6, at 8:22, 9:00, 9:45, 10:05, 10:12, 10:15, and 10:29. Usually these were bouts of 6 to 8 songs delivered from a tall 30-foot tree east of the nest site but overlooking it. Twice he sang in a tree directly above the nest at 20 feet and once in a 10-feet tree directly above the female as she gathered material on the ground. On one occasion he drove off another bird at the border of the territory and then sang there. On December 8 he drove out another sparrow but gave no song and later, when the female was not gathering material, he moved about on the ground with her. The longest song bout comprised 20 songs in succession at 7 to 8-second intervals.

NEST SITES

Nests in the pasture and forest-border vegetation that *capensis* inhabits are placed either in low bushes and grass tussocks or on the ground. Of 19 nests of which we made some record at Santo Domingo, 13 were in bushes or in tangles of bushes (pl. 4, *a*), ferns, and grass, 2 were in a tuft of grass or cane above the ground (pl. 4, *b*), and 4 were sunk in the ground among grass or low dense ferns, moss, and forbs. The ground nests were all on sloping ground and two were in turf at the crest of road cuts which dropped off 5 to 7 feet below. The nests above ground were at heights of about 1 foot (four cases), about 1 ½ feet (two), about 2 feet (three), and about 2 ½ feet (six). All nests were screened from above by a cover of leaves or grass, usually quite completely so. Four of the nests were placed in hydrangea plants, all by the same female, number 485, and all were about 30 inches up in crotches and rather poorly concealed from the side and below because of the open growth of this plant. The two nests of female 488 were in a bush and in the turf, respectively.

NEST STRUCTURE

The nests consist of a grass and stem cup and base and a lining, the two parts usually not sharply set off from one another. The nests lack any significant basal platform or stick foundation. Nor is there any firm attachment or weaving of the material around bush supports.

The main cup is either composed entirely of grass or it may contain leaves, stems of other plants, and some rootlets (pl. 4, *a*). In one nest a clod of earth 2 cm. across was still on a grass plant used and in another instance several small clods were attached to rootlets that were incorporated. Wet and weathered plant material with some mud adhering was put into the nest by female 485.

The nest lining consists of fine grass or grass and hair. We recorded three instances of substantial amounts of hair, yet many nests are without it. In one hair-lined nest a nestling had gotten a hair down its throat and had to be rescued. No felting material was ever used, and only occasional feathers were present, usually derived from the birds themselves. One captive on one occasion when many chicken feathers were available used a number of them, but nests in the wild near chicken yards were without such feathers.

Dimensions in inches of four nests were: outside 4 across and 3 deep and cup 2 across and 1 ¾ deep; 3 ½ × 2 and 2 ¼ × 1 ½; 4 ½ × 2 ½ and 2 ½ × 1 ½; 4 × 3 and 2 ½ × 1 ½.

The cup of the nest is usually tightly packed by the usual procedure of the bird sitting in the nest and pressing outward, so that the whole structure is firm. At one nest, the small bush in which it was situated drained water down the branches into the cup. Its structure was so compact that water stood in the nest several hours after a rain, resulting in the immersion of the eggs. The nest was then deserted, possibly for this reason.

The nest of female 485 built in early December became loosened and tipped when the young were five days old either as a result of wind or unequal growth of supporting plants in which it was not well braced. The nest would have failed at that time had we not wired it in place. Nests in captivity sometimes develop similar defects of placement or construction.

One nest from which young fledged was heavily infested with mites which persisted in the dense nest structure for several weeks.

EGGS

Number.—Evidence from the field in Colombia shows 2 eggs to be the normal clutch for this equatorial population. Fifteen nests contained this number of eggs or young under circumstances indicating the clutches were completed and had not been reduced by predation. One nest held a single small young but there is no assurance that this reflects a one-egg clutch. We never saw adults with more than two young in attendance and indeed the prevailing situation was one in which there was survival of but a single young to the stage of following the parent. Carlos Lehmann tells us he has seen a three-egg clutch and there is no reason to suppose that this does not occur in a small number of instances.

In captivity the clutches laid at Berkeley were as follows: 1 egg, 19; 2 eggs, 60; 3 eggs, 6. Occasional losses of eggs to mice in the cages may account for several 1-egg clutches and at least 9 of them were the products of female 498 at times when she was at least 7 and 8 years of age. The 3-egg clutches occurred only from late May to early July, all during the middle of the prolonged laying period, the extension of which is apparently stimulated by long photoperiods (Miller, 1965). It is possible that these photoperiods may have stimulated these large clutches also as there is a suggestive grouping of them about the summer solstice. Three different females were involved in producing the 3- and 1-egg clutches, and each of them usually laid two eggs.

At temperate latitudes in Chile, in other races of the species, 3-egg clutches are the rule and some of 4 and 5 occur (Goodall, Johnson, and Philippi, Las Aves de Chile, 1946) and in the Museum of Vertebrate Zoology there are 3-egg clutches from the Río Negro district of Argentina and from Minas Gerais in Brasil and a 4-egg clutch from Costa Rica.

Appearance.—The background color is usually pale blue or blue green but it may be whitish or cream and occasionally strongly blue. The spotting is usually fine and rather evenly distributed, yet in some there are fairly well formed wreaths and heavy clusters of brown and drab spots, some up to 2 mm. across (pl. 4, *b*). Despite the very considerable individual variation, the prevailing resemblance of the eggs is to those of *Zonotrichia leucophrys;* many would be indistinguishable although the more heavily marked and rather uniform spotted extreme types of *leucophrys* seem not to be duplicated in *capensis.* Series of song sparrow eggs are less uniformly spotted and have heavier blotches, the latter features setting off most eggs of fox sparrows also.

Size.—Measurements of 26 eggs from the Colombian population show no evident differences between those laid in the wild and in captivity nor

between clutches of 1, 2, or 3 eggs. The average dimensions in milimeters are 20.1 long and 15.2 wide. The eggs showing extremes measured **21.6** × 15.0, 20.3 × **16.4**, **18.5** × 14.7, and 18.7 × **13.4**.

Laying.—So far as our records show all eggs are laid in the early morning within two hours of daybreak. Eggs appear on successive days in the morning. This was verified three times in the laying of two-egg clutches in the field and it was determined approximately 30 times in the clutches laid in captivity, involving both 2-egg and 3-egg clutches.

There may be exceptions to the laying on successive days. Three times in captivity two days appeared to intervene between the laying of two eggs but in none of these instances was a check of nests made in the late morning of afternoon of the day that intervened. Either the second eggs were laid late on the succeeding day or a whole day was skipped.

In one instance a captive female was flushed from a nest at 8:15 a.m. on July 7 and the egg under her was so recently laid that it was still wet.

Laying seasons.—As discussed at length elsewhere (Miller, 1962, 1965), laying in the field study area in Colombia occurs throughout the year with two peak periods. This seasonality is modified (Miller, 1965) in these same birds in captivity under the photoperiods of north temperate latitudes into one prolonged breeding period with a winter non-breeding interval.

INCUBATION

Incubation starts with the laying of the second egg. Whether or not the female stays on the nest on the night preceding its laying we have not determined, but the usual nearly simultaneous hatching of the two eggs suggests no effective incubation in those instances on that night, and there is none during preceding daylight hours.

All incubation is performed by the female and she is not brought food by the male at the nest or elsewhere.

Incubation sessions.—Data on sessions were recorded at the nests of female 485 primarily, as the sites of her nests afforded opportunity for undisturbed watching whereas almost all other nests with eggs were not favorably situated. The records of attentiveness of this female were derived in the period when the eggs had 4 to 6 days of incubation. Two nestings of the same individual, one in May and the other in December were involved (figs. 5, 6). The length of the attentive periods might suggest some differences in the forenoon periods for these two nests but the variability is such on any one day that this apparent difference is not at all valid statistically.

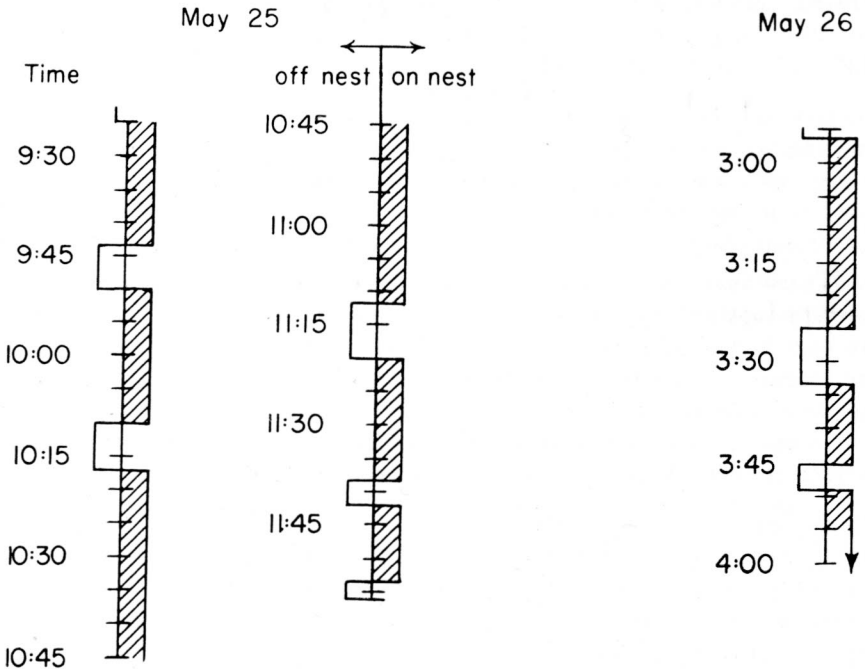


Fig. 5. Incubation of female 485 in sample observation periods on May 25 and May 26; eggs at 4 and 5 days of incubation.

The 16 complete and undisturbed attentive periods timed ranged from 12 minutes to 59 minutes and averaged 30 ½ minutes. The distribution of these however is bimodal (fig. 7), one main group having a mode in the 18 to 27-minute range and a second group in the 55 to 59-minute range. Long and short periods both occurred in the morning but none of the long group was in the afternoon. In the morning there was no correlation with temperature or weather. One of the shorter periods occurred in the early morning on December 18 at a temperature of 59°F whereas during long sessions on the morning of December 17 temperatures were 61° to 62°. The short period early in morning in the instance recorded probably was stimulated by hunger.

That attentive periods may be longer is shown by a record of female 487 which had one two-hour attentive period from 9:35 to 11:35 a.m. followed by a 25-minute inattentive period, reflecting in both types of period some substantial variation between individuals and indicating that caution must be taken in assuming any very sharply defined species characteristics for incubating sessions in the absence of large samples of data that can be statistically treated.

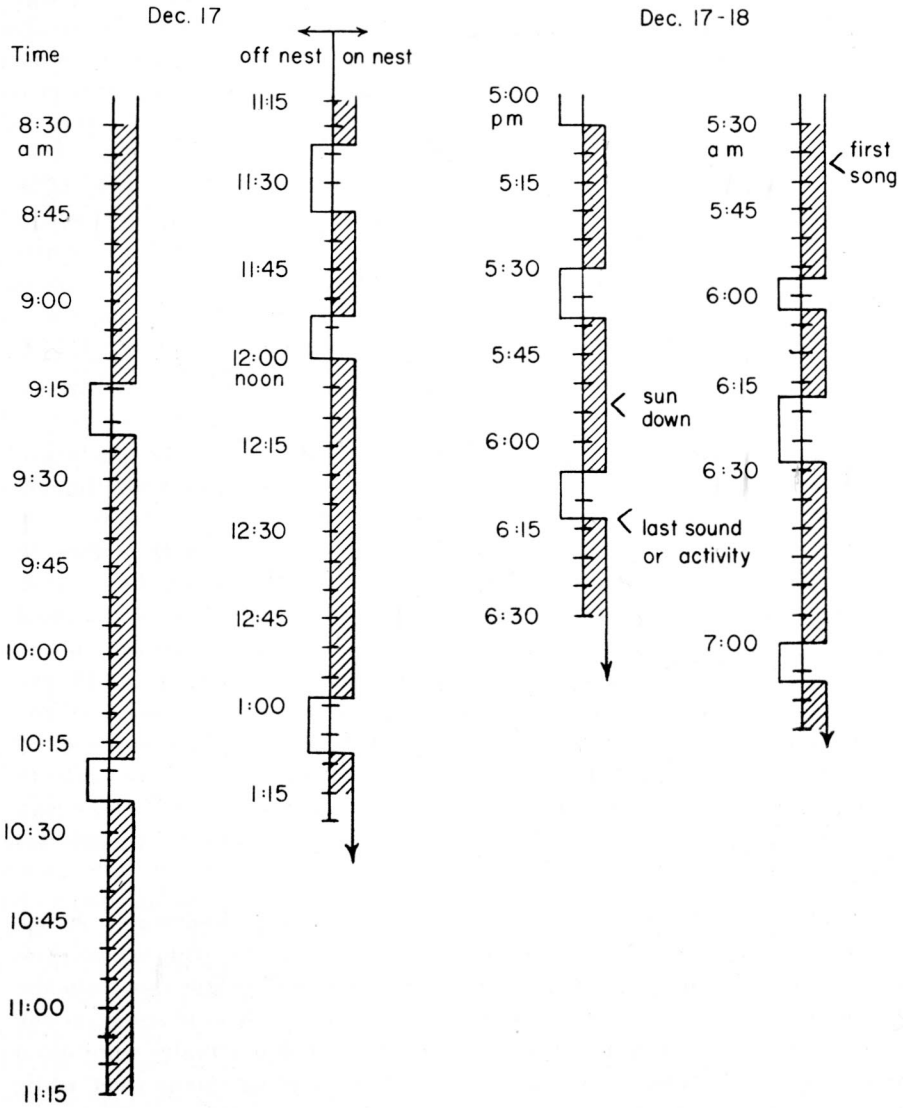


Fig. 6. Incubation of female 485 in sample observation periods on December 17 and 18; eggs at 5 and 6 days of incubation.

The inattentive periods show a narrower variation than the attentive periods. They ranged from 2 to 12 in female 485 with an average of 7 2/10 minutes and a predominance of values of 7 to 9 minutes. The distinctly short periods followed either short attentive periods or represented the

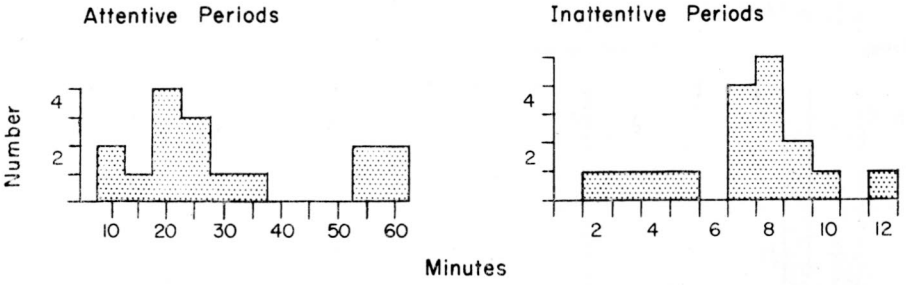


Fig. 7. Frequency distribution of completed incubating sessions and inattentive periods of female 485. Records combined from observations of two different nestings (see figs. 5 and 6).

first early morning nest departure. Sessions off the nest regularly are used for feeding and stretching and preening; on one ocassion the female bathed during a mid-day (11:53) inattentive period.

The nighttime duty for female 485 was ascertained on December 17 and 18. It was 11 hours and 44 minutes long and began as the last sounds and actions of zonotrichias were noted at 6:13 p.m. It continued until 5:57 a.m., twenty minutes after the first songs of the sparrows in the morning. There was essentially 10 hours of daytime coverage or 81 per cent, based on data for average length of attentive periods. This with the night coverage makes 21 hours and 44 minutes for the daily cycle. Viewed another way, the female achieves her own food intake in 2 hours and 16 minutes daily; whether or not this intake is in balance with expenditure of energy at this time is not known. She may have some moderate fat reserves available.

Behavior.—Female 485 left her nests in the hydrangea hedge voluntarily either in a direct flight into the open or by slipping off into the bushes. Her arrivals were usually rather obvious as she flew into the bushes within a yard of the nest and the bushes of this type shook as she moved on to the nest under cover of the foliage. Other females were often much more cautious in going to the nest, moving many feet while concealed by the bushes. Female 487 with a nest on the ground in the grass alighted 15 feet away and went by foot to the nest, rather inconspicuously but not completely hidden.

Female 485 was never joined by her mate while incubation was being observed. He sang from his high song post nearby, and on the early morning of December 18 he sang there as other males first sang in the period before the female left the nest. Female 487 was with her mate during an off-duty period and the male sang a little at this time. In

captives, the male often goes to the female as she leaves, sometimes aggressively, and then accompanies her and gives pair association notes, resuming prominent singing when she again settles on the nest. We have never seen a male actually go with the female to the nest as she returned for duty.

Female 485 usually went 50 feet from the nest to a foraging area where garden debris and other scraps were dumped. Occasionally she foraged nearby in the garden but not close to the nest where she had gathered much of the nest material earlier. On several relief periods she mounted a small tree near the nest to heights of 15 to 20 feet and sat preening.

Length of incubation period.—The one fairly precise determination of incubation period in the field fortunately involved female 485 for which data were obtained on incubating attentiveness. Her December nest received the second egg on the morning of December 12 before the hour of 8:30 at which time she was flushed from the nest. At 4 p.m. on December 23 one young was hatched and its down was dry. On December 24 at 8 a.m. the second young was found to have hatched; possibly it could have hatched late on the 23rd but this is unlikely. The standard incubation interval, from last egg laid to last hatch, was therefore 12 days. The other egg may have hatched in 11 days and about 8 hours unless some heat was applied on the day or night when this first egg was alone in the nest.

In captivity incubation periods in outdoor enclosures were checked closely when possible and 11 determinations made as shown in table 1. These periods are all figured from time of laying of the last egg to the hatch of the last egg when all eggs hatched. When times are stated in even days, young and eggs were found at about 8 a.m. All calculations unless otherwise noted have an accuracy of about 2 ± hours. In addition other determination where not all eggs hatched indicated periods of 11 days, 11 days and 7 hours, 12 days, and 12 days. We had no sure evidence of any incubation extending to 12 ½ or 13 days.

The most precise determination was made on a nest in captivity in which the eggs were marked. Here the first egg hatched in the morning 11 days from the start of incubation or 12 days from laying, and the second egg hatched the same afternoon at 11 days and 7 ± 1 hours.

Hatching.—Most young hatch in the morning, although in the case of 485's nest in December, the first egg hatched sometime between 11:40 a.m. and 4 p.m. In her nest of June, one young had hatched at 7:30 a.m. on the 2nd and the other young was half out of its shell. The first young had not hatched by 4:30 the preceding afternoon and almost certainly it hatched early on the morning it was found as its down was dry at 7:30. The second young had almost entirely freed itself of its shell by 7:50 and

the shells of the first egg had been removed by the parents. The record of captive incubation periods similarly reflects a predominance of morning hatches.

Prompt removal of the egg shells is usual, as in most passerines. In one hatching in captivity the male removed the shells rather prematurely, although certainly the females usually take care of the removal. In this instance the hatching was occurring at 4 p.m. One young was in the lower part of the shell with part of the shell cap still slinging to its head. The young soon kicked out of the lower half and made an unsuccessful effort to reach the piece on its head with its foot. The second egg then opened around its entire circumference and in about four efforts the young was largely free. As the observer retreated, the male went to the nest and took the lower end of the first egg shell, flew across the cage and then ate it. He returned, took another shell fragment and ate it near the nest. He next removed the young with the piece of shell attached to its head and placed them on a board at the front of the cage and pecked at the shell on the chick's head. Failing to remove it, the male returned to the nest, picked up the larger lower part of the shell of the second egg and flew out from the nest, the young dropping out of this shell to the floor; the male then ate this shell. The male did not attack the young, which we had to return to the nest, but he seemed most eager, indeed too eager, to remove and eat the shells.

NESTLING STAGE

The brooding period.—Brooding by the female is almost as continuous as incubation in the first three to four days after hatching. Food deliveries by the female, or by the male when he is a bird that does participate, are surprisingly few.

Female 485 who received no assistance from her mate at any time, showed the following partial record of activity during the brooding stage at her nest of early June. When the young were one day old on June 3, she was off them at 7:05 a.m., foraging. She may have fed them once or twice during the first hour of daylight, as the young did not gape at this time. The female returned to brood at 7:20 and she may have fed them then. She was delayed about 10 minutes by our actions. A brooding session of about 50 minutes ensued and then a period off the nest of about 14 minutes. On returning, she fed the young, picked up feces, and left, returning in another 4 minutes without feeding and settling for brooding.

Later at 9:50 the bird was brooding and stayed 58 minutes until she left voluntarily. In the interval she had shifted position on the nest twice. Thus there were two brooding sessions of 50 minutes or more-

equivalent to the longer type of incubation sessions this bird had shown. Feeding was again seen at 10:56, after the female had been off for 8 minutes. At 10:50 after a long brooding, the young opened their mouths as we jarred the nest in parting the leaves above it.

Feedings seemed to occur, then, about, once an hour during the entire forenoon. Although there were some discontinuities in our observations, it is unlikely that more than 6 deliveries were made. Food could readily be obtained by the female, both for herself and young in 8 to 10 minutes. What she brought to the young at this stage was small and only once was visible outside the bill, when we could see parts of moths.

On the following day, with the young two days old, there was a long brooding period again, from 7 a.m. on, for at least 57 minutes. About 13 minutes was then used in relief and foraging, with feeding following and resumption of brooding following the eating of a fecal sac.

When the young were three days old, two feedings were observed at 11:44 and 12:01, with no brooding between, but earlier there had been a brooding session of 25 minutes which had been accidentally terminated by us.

The later nestling period.—When the young were five days old on June 7 feeding was more frequent and brooding was reduced to judge from a watch kept from 8:45 to 9:34 were made at 8:58, 9:08, 9:17, and 9:34 with stays at the nest of only 1 to 4 minutes at each visit. This period of development of the young is of course approaching the time of greatest food demand for growth, and feathers were beginning to break out of the sheaths on the body areas. The feeding rate in the morning may have been about 4 an hour as against 1 an hour at the age of one day.

At the nest of this female in December, when her young were seven days old, the feeding rate in the morning had risen further, probably to a maximum for the nestling period. In an interval of 95 minutes from 8:25 to 10 a.m., there were 9 food deliveries. The intervals were irregular (fig. 8), showing ability to gather and deliver food by this one parent in as short a time as 4 or 5 minutes, although the loads of food appeared rather small. The hourly rate was about 6. At no time did the female brood in the course of this watch.

Participation of male.—In all the watching of the nests of young of female 485 her mate was never seen near the nest nor gathering food in the bill as though he intended to bring food. Neither did he participate in feeding the fledglings or the fledgling cowbird which this female raised on one occasion. He was however regularly in the territory, occasionally singing and challenging trespassing males.

The attendance of young at the nest of male 460 and his first and second mates in February and June, respectively, showed similar feeding

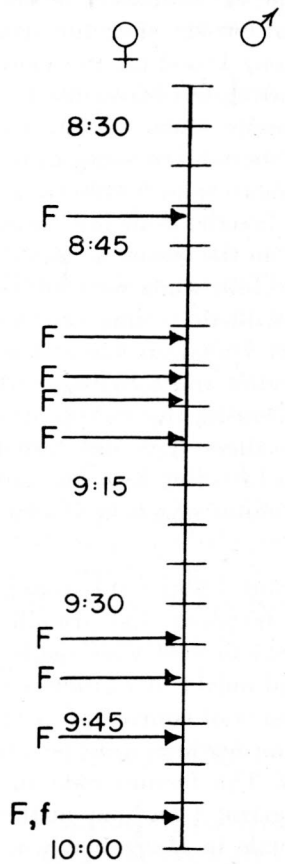


Fig. 8. Food delivery at nest on morning of December 31. Nest of female 485, containing two 7-day-old young; no participation by the male. F, indicated food delivery; f, removal of fecal sac.

rates at comparable stages of development of the young to those of female 485, but there was a major participation by the male and a much more frequent association of male and female in foraging together and guarding the nest as well as in bringing food and in removing fecal sacs.

Their nest in February had one young only which was judged to be 5 days of age on the 16th. For more than an hour following a brooding session the female was not on the nest nor was food brought (fig. 9). Then from 9:15 to 10:15, 4 food deliveries occurred in the hour, 2 by each parent. This seems comparable to the 4 per hour delivery at 485's nest with young five days old. In this case but a single young was involved and the long inactive period from 8:15 to 9:15 may have reflected this fact.

In any event the two parents individually were doing very much less, because of sharing duties, than 485 had done.

On February 18 when the young was 7 days old, we saw only the female bring food and then only twice between 8:50 and 9:25. Because of human disturbance in the area, she delivered only once. In the hour preceding she had spent much time foraging for herself in rather leisurely fashion and often together with the male on the ground. The male on this morning was active on several occasions in driving off other birds and in singing, and he delivered no food in the course of a watch of an hour and a half. He did tolerate a streaked juvenile that moved and foraged through his territory.

In the nest of June with mate 488, when the two young were 4 and 5 days old, male 460 seemed to do most of the feeding. As seen in fig. 10, the female had a brooding session up to 9:23 which terminated when the male came in with food. The female then foraged for herself or with the male in the grass for long periods. She may have sneaked to the nest once undetected, for she was brooding at 10:25 when the male again brought food, and at 11:03 she was carrying food but was chased away by the male; she gave defense screeches as he closed in on her. Twice before in the morning there had been chases and screeches. Thus for one reason or another the female delivered food at most only once between 9:10 and 11:25, but she brooded twice and the male delivered food 5 times. The feeding rate was therefore about 3 per hour.

Again on the following day, the female was off the nest entirely from 8 to 12 and with the male for long periods, spending much time in foraging for herself and in preening. She was more difficult to follow than he and might have sneaked through the bushes twice with food when we briefly lost track of her. The male brought food 5 times and even if the female brought food 2 or 3 times undetected, the rate of delivery over the whole 4-hour morning interval was only about 2 an hour and thus surprisingly low.

This pair and female 485 may have had different times in the day of peak feeding activity, for with both birds working, the pair may have fed their young better in early morning before our observation periods than did female 485. The pair may also have brought larger amounts per trip than did female 485. Unfortunately the nest of 460 and 488 was not watched when the two young were 7 days of age when food deliveries should have reached a peak.

In any event the participation of male 460 in feeding was conspicuous and seemed to be greater than that of his mate 488. It had been at least approximately equal to that of his former mate 462 when they had a single nestling.

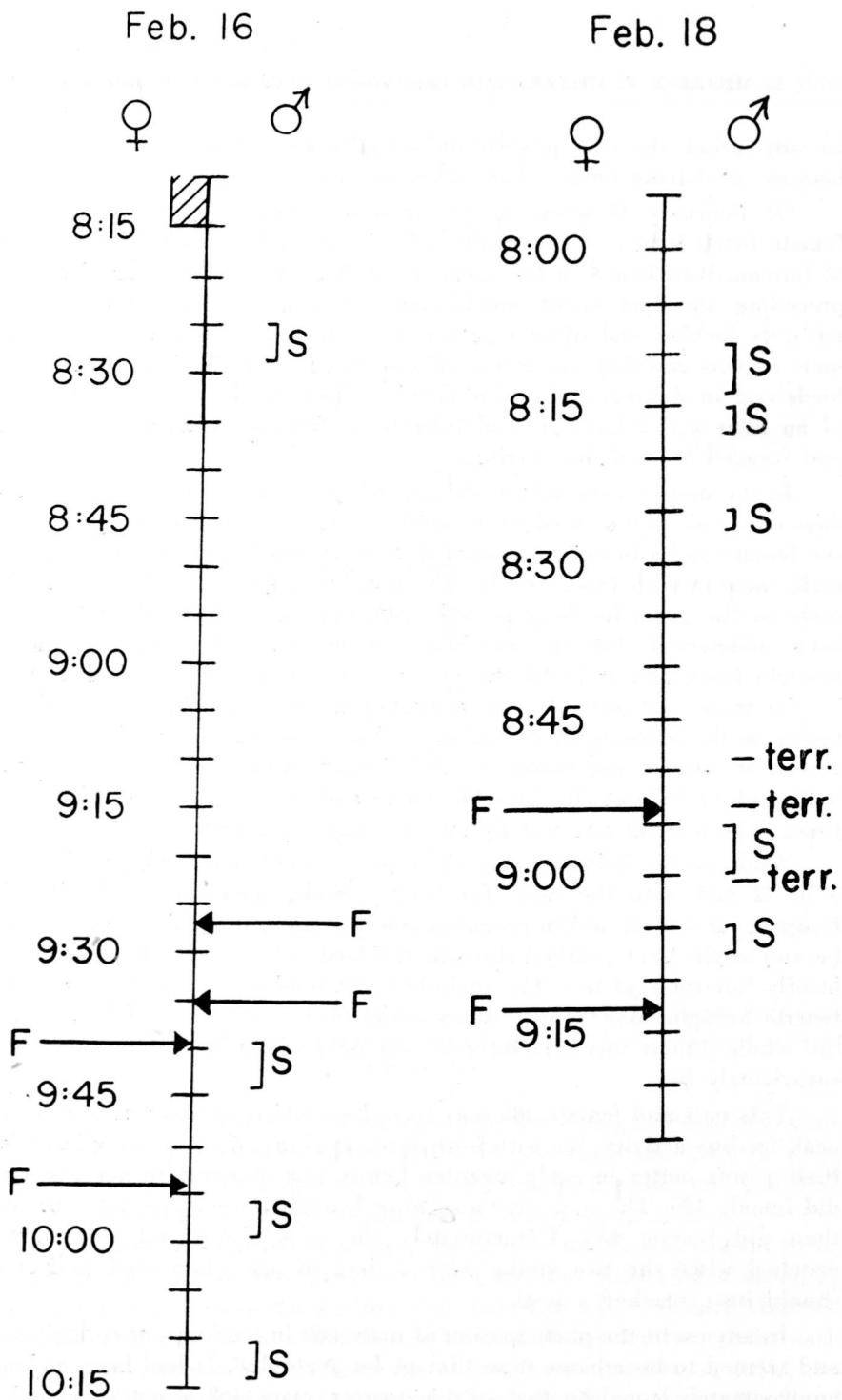


Fig. 9. Food delivery and activity at nest tended by male 460 and female 462 on February 16 and 18 with a single young, 5 and 7 days old. F, feeding of young; s, song bout of male; terr., territorial defense chase.

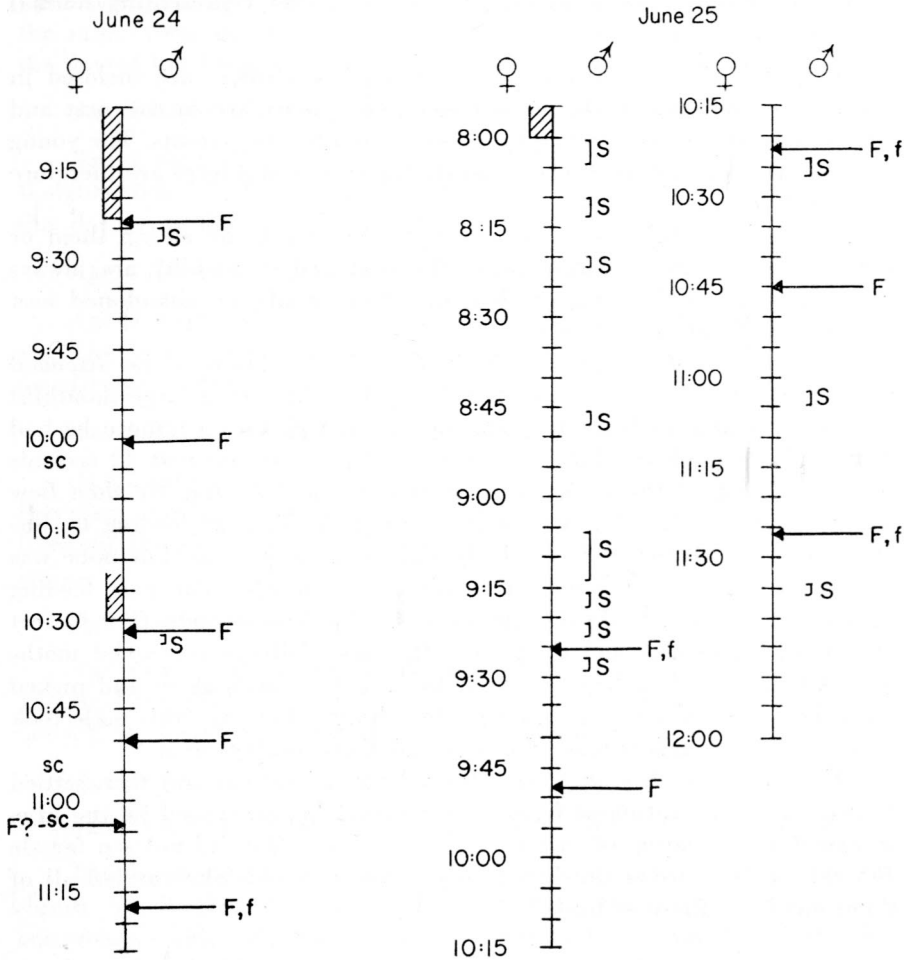


Fig. 10. Food delivery and activity at nest tended by male 460 and his second mate, 488, on mornings of June 24 and 25 with two young 4 and 5 days old, respectively. Symbols as in figures 8 and 9; also, sc indicates defense screech and shaded areas mark brooding periods.

In captivity three males varied somewhat in the degree to which they fed nestlings, but the pattern of food deliveries in the cages is judged to be much influenced by confinement, food availability, and food type such that natural activity is not seen. We did note captive males feeding young on the day of hatching. In one captive male, the bird was seen to settle on the nest for about 2 minutes following feeding when the young

were 5 days old. This is an exceptional event, not representing normal behavior.

Disposal of feces.—Feces, as in related sparrows, are inclosed in gelatinous envelopes in the period when the young are in the nest and accordingly are readily picked up and removed by the parents. The young from an age of two days at least, elevate the cloaca, and feces are therefore presented for easy removal.

Disposal of fecal sacs is accomplished either by eating them or carrying them away to drop them. The nest and its vicinity are always kept clean up to the time of fledging. Occasionally an abandoned nest has the last fecal sac left in it.

Male 469 on June 25 was watched especially closely as he attended the nest of five-day old young. At 9:26 he flew in with a large mouthful of food in which small moth wings were visible. Within a minute he had worked in through the bush to the nest. He was at the nest 12 seconds while the necks of the young were upstretched and waving. He then flew off carrying a fecal sac and by 9:29 he sang. At his next feeding he was at the nest 31 seconds and seemingly waited for a fecal sac but none was passed. In the feeding contact he made 3 vibrant jabs. The next feeding appeared to be a small beak-load. He fed twice in 6 seconds, flew 60 feet west with a fecal sac and then sang. His next delivery contained moths and at the succeeding trip he was at the nest 6 seconds again and picked up a fecal sac and ate it at the nest. On the previous day this male took a sac to a perch 2 feet from the nest and there swallowed it.

Female 485 with young two days old ate a fecal sac and then settled to brood, yet the eating of feces cannot invariably be caused by the urge to brood as the eating of sacs by the male shows. We did not see female 485 eat any sacs when she had young seven days old. She carried all of them out from the nest bush.

DEVELOPMENT OF YOUNG

The appearance and development of the young are closely similar to that of young of *Zonotrichia leucophrys* which Banks (1959) has described in detail from many observations. Our less extensive data on *capensis* (wild birds, and well fed, vigorous captives) are here reported only briefly where confirmation of the similarity to *leucophrys* seems meaningful or where departures may be reflected. A variable number of weights were recorded at different ages.

Age 0 days.—We noted that the skin was orange rather than pink, turning to yellow; this color was noted even while the young *capensis*

were partly in the shell. The down is dark gray-brown and occurs in the same areas as in *leucophrys*. Weight: 2.7 gm. Feces are passed on the day of hatching, at least in the afternoon following a morning hatch.

Age 2 days.—The red mouth is conspicuously yellow rimmed.

Age 3 days.—The primaries extend beyond the skin ½ to 1 mm. Weights: 6.8, 7.7., 7.8, 8.3 gm. Slightly open eye slits may first appear on this day or on the succeeding day.

Age 4 days.—Primaries 1-3 mm. long. Weights: 8.1, 8.7, 8.8, 10.9 gm.

Age 5 days.—Primaries 3-5 mm. long. Weights: 9.6, 10.0, 11.1, 13.8 gm. The body feathers begin to break from their sheaths, but they form no effective covering.

Age 6 days.—Primaries 7-10 mm. long. Weights: 13.0, 15.9, 16.8 gm.

Age 7 days.—Primaries 10-15 mm. long. Weights: 15.7, 18.1, 20.0 gm. Preening and fear reaction were noted. The primaries begin to break from the sheaths at the tips. The back feathers form an effective covering layer.

Age 8 days.—Primaries 16-20 mm. long. Weights: 16.2, 19.0, 21.0 gm.

Age 9 days.—Primaries 17.5-24 mm. long. Weights: 17.9, 19.8, 20.0 gm. The loud fledgling *chip* was first given by captive young, birds which had not left the nest cup and thus had not fledged.

Age 10 days.—Weight: 20.0 gm.

Age 11 days.—Primaries 25-31 mm. long. Weights: 19.1, 22.7 gm.

The limited data on weight plotted as averages fall along the line shown by Banks (fig. 11) and reveal no significant departures from *leucophrys*. Although the greatest growth rate in the young of these species is in the first 3 or 4 days of life, the total food requirements are greatest when they are larger, approaching adult weight, and still showing substantial daily growth increments, at 6 to 7 days of age. The reaching of a plateau in weight at 9 to 11 days is also clearly shown (fig. 11). Compared with the well-studied vesper sparrow (Dawson and Evans, 1960), this is attained about 2 days later.

The growth of the primaries in *capensis* again falls within the limits of variation for *leucophrys*. Daily increments were of the order of about 4 mm. No slowing of growth as fledging was approached are reflected in our figures, although Banks thought this might occur.

Fledging.—The age at fledging is complicated in its determination by the degree to which premature departures from the nest owing to

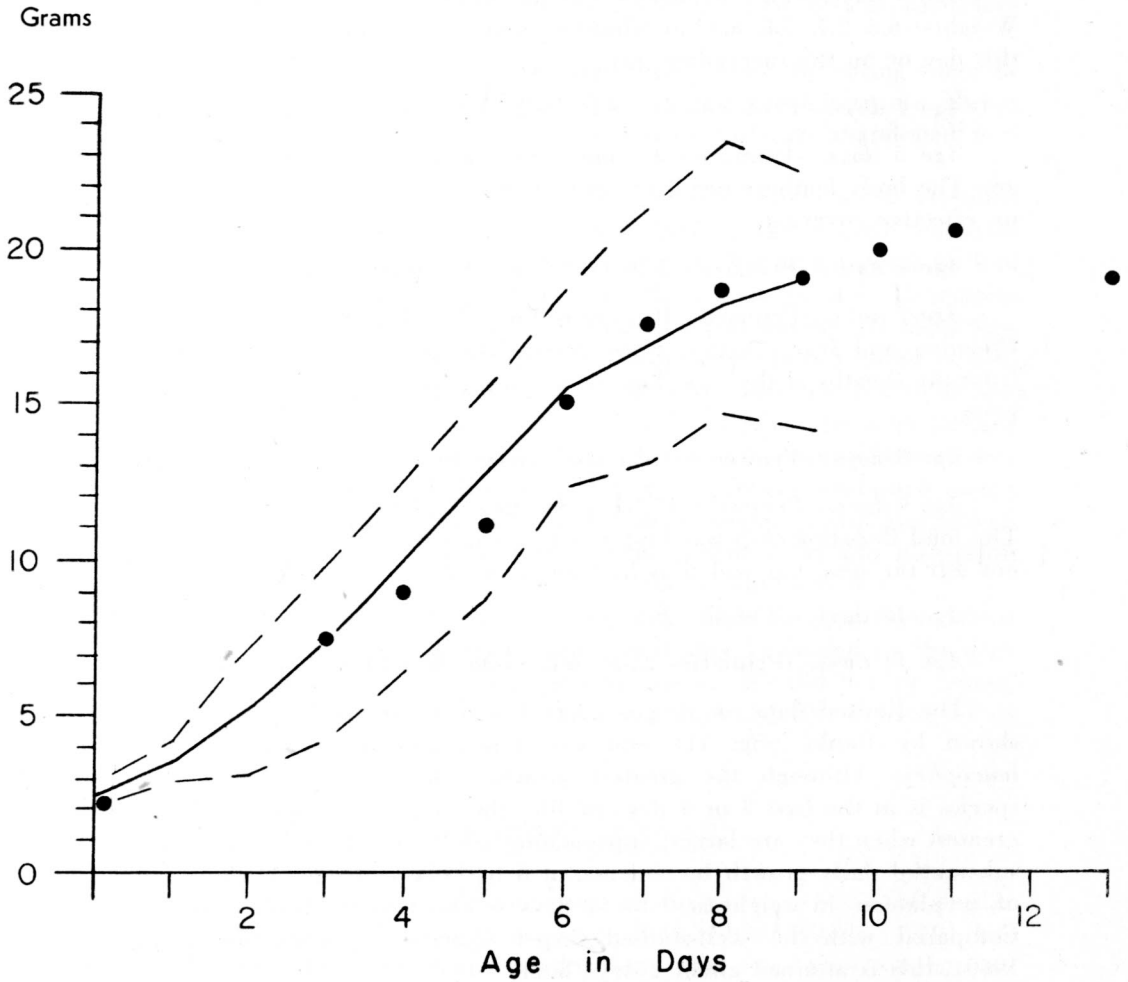


Fig. 11. Development of young, comparing data for *Zonotrichia leucophrys* and *Zonotrichia capensis*. Solid line, mean daily weights of nestling *leucophrys* and range of variation shown by dashed lines (data from Banks, 1959: fig. 1). Dots represent weights or mean weights (see p. 117) for same ages for *capensis*.

disturbance enter into the record. This factor and the natural variability in time of development of the nest-leaving restlessness make it necessary to draw comparisons with special care. Blanchard reported data on fledging of *Z. leucophrys pugetensis* (1941), and it is thought that our records for *capensis* are comparable even though part of ours are derived from nest-leaving among captives that were accustomed to being fed by us and were not frightened; neither were they retarded in their rates of growth and development.

The apparent later fledging in *capensis* as indicated in table 2 is probably meaningful biologically but it will not stand a rigorous statistical test. It is safe to say, however, that *capensis* at least does not fledge earlier than *leucophrys* despite the fact that clutches are usually 2 rather than 4 as in *leucophrys*.

Discussion.—The food delivery rate for nestling zonotrichias in general may be taken as fully satisfying their demands. When hand-raising them, it does not seem possible to speed up development and the attainment of fledging by offering unlimited amounts of food. We do not have data on food delivery rates at nests of *leucophrys*. But the slow rates of about 6 nest visits per hour in *capensis*, when two young are present at the stage of maximum requirement, must be significantly slower than in *leucophrys*. In *Melospiza melodia*, for example, feeding rates reported by Haldeman (1931) at the time of maximum requirement average about 17 per hour with 3 young present.

But despite the slow feeding rate, young *capensis* do not lag behind the young of the related *leucophrys* in weight or feather growth. Perhaps there is compensatory delivery of larger amounts of food at each visit but this is not at all indicated by subjective judgment of what can be seen in the bills of parents of the two species as they go to their nestlings. The nestlings of *capensis* do lag behind apparently in fledging time in the maturation of the requisite instinct.

The presumption that tropical latitude species are subjected to especially great nest predation, and therefore that visits to the nest by the parents if minimized leads to better survival, must be balanced off against the longer period that the nest is occupied if fledging is delayed. Actually in *capensis* we have inadequate data to support a view that nest predation is exceptionally high. There is great loss of young following fledging (see p. 142) and there may be selective advantage in delaying fledging somewhat to attain a better maturation of neuromotor mechanisms by the young in preparation for that critical time.

FLEDGLING STAGE

When the young fledge, they at once go into the dense bush or grass cover and move chiefly by hopping. They can flutter a few feet if tested, but they fly awkwardly or weakly at best. In the protecting vegetation they have no need for wing action to carry them more than a foot or two at most. The young stay away from openings and below the bush tops. Food is delivered regularly to them, the parents coming in cautiously as to a nest. A well-fed juvenile only occasionally moves or gives the location note. If the parents are long detained or are lost, the young hop about under cover calling vigorously and continually.

In this concealed hopping stage, the young must be especially vulnerable to predation, presumably from snakes and weasels, and it is rare (one case) that more than one young from a nest appears subsequently to follow the parents in the open. At the well-observed nest of 460 and 462, the fledging was 11 days from hatching and the juvenile did not emerge from cover to follow the parents openly until 10 days later and thus at an age of 21 days. Two other young from nests near our house first were seen in the open at about 23 and 24 days of age.

In captives, this period of normal concealment can be followed to ascertain development of feathers and of significant behavior. The best sequence of development was seen in a vigorous young male of 1960 that fledged at 12 days and then began hopping about and fluttering against the wire of the cage. At 16 days it was starting to peck at food and gravel in an exploratory and ineffectual manner. At 18 days it "discovered" the water dish and drank and fed itself a little on mash. At 19 days it was picking up substantial amounts of mash and gravel and it took its first bath. At 23 days it attacked and ate 3 meal worms. This is then the degree of self sufficiency, still mixed with regular begging, which is attained at the natural emerging period when young begin to fly about after the adults.

The aforementioned captive had a standard wing length of 64 mm. and a tail length of 50 mm. at this stage. The wing of this bird reached 65 mm. and terminated growth 3 days later. Consequently the wing area is virtually complete at the time young move into the open whereas at nest leaving it has only 80 per cent of its ultimate linear dimension. The tail, however, was not full length, but continued growing about another week, reaching 56 mm. In the 10 days of postfledging growth there is no gain in weight and often some slight loss. The rate of increment to the wing is about 2 mm. a day and the tail almost 3 mm. a day until a slowing in the last 2 or 3 days just before definitive length of each is reached.

In captive young when two survived, within two or three days of fledging the young fought each other vigorously and it was necessary to separate them. Such fighting would not normally occur in the wild, but if it did, it would at least lead to the separation of the young such that they would be less vulnerable to predation. The reaction may then have some adaptive value.

In the wild, when young emerge, they follow the parents in flight and drop to the ground with them as they forage, giving location notes repeatedly. On March 3 such a newly emerged bird fed itself, rather ineffectually it seemed, and was tolerated within a few feet by both the male and the female. Two days later, when 23 days old, we also saw it being fed. It was last seen to be fed when 33 days old, although it did not give a begging note then. Two days later it was still in the territory with its father but it was not again found; probably it moved away on its own at this time when it was about 35 days old. However, another juvenile of this same male stayed with the father to about 40 days, continuing to beg and receive food from the male and his mate. Young of female 485, whose male never assisted at the nest, likewise received no aid from him during the postfledging period. He did not, however, attack the juveniles or appear to drive them away.

In the captives at 26 days of age young were taking and cracking some seeds and were largely self-feeding at 29 days, but they begged occasionally to 33 days; they stopped this completely at 35 days. Real dependency seems then to last to about 28 days—a four-week period—, after which young probably could survive on their own, although gaining benefit from the parent and some protection in warning and association for another week at least. The timing of independence does not seem to differ from that in *Zonotrichia leucophrys* either at latitude 38°N (Blanchard, 1941: 32) or latitude 62°N (Oakeson, 1954: 361).

INDEPENDENCE AND ESTABLISHMENT OF YOUNG

The independent streaked juveniles wander and readily move through territories of established adults. They and molting adults seem at times to form loose foraging aggregations. These often center in neutral feeding areas or are only mildly challenged by territorial males.

The young birds start the postjuvenal molt at the time of independence or within about 10 days after, and it is estimated that this molt normally occupies about two months, with a probable range from 50 to 100 days (see Miller, 1961). The age at which the young complete this molt is then about 4 months, at which time they are indistinguishable in appearance from adults.

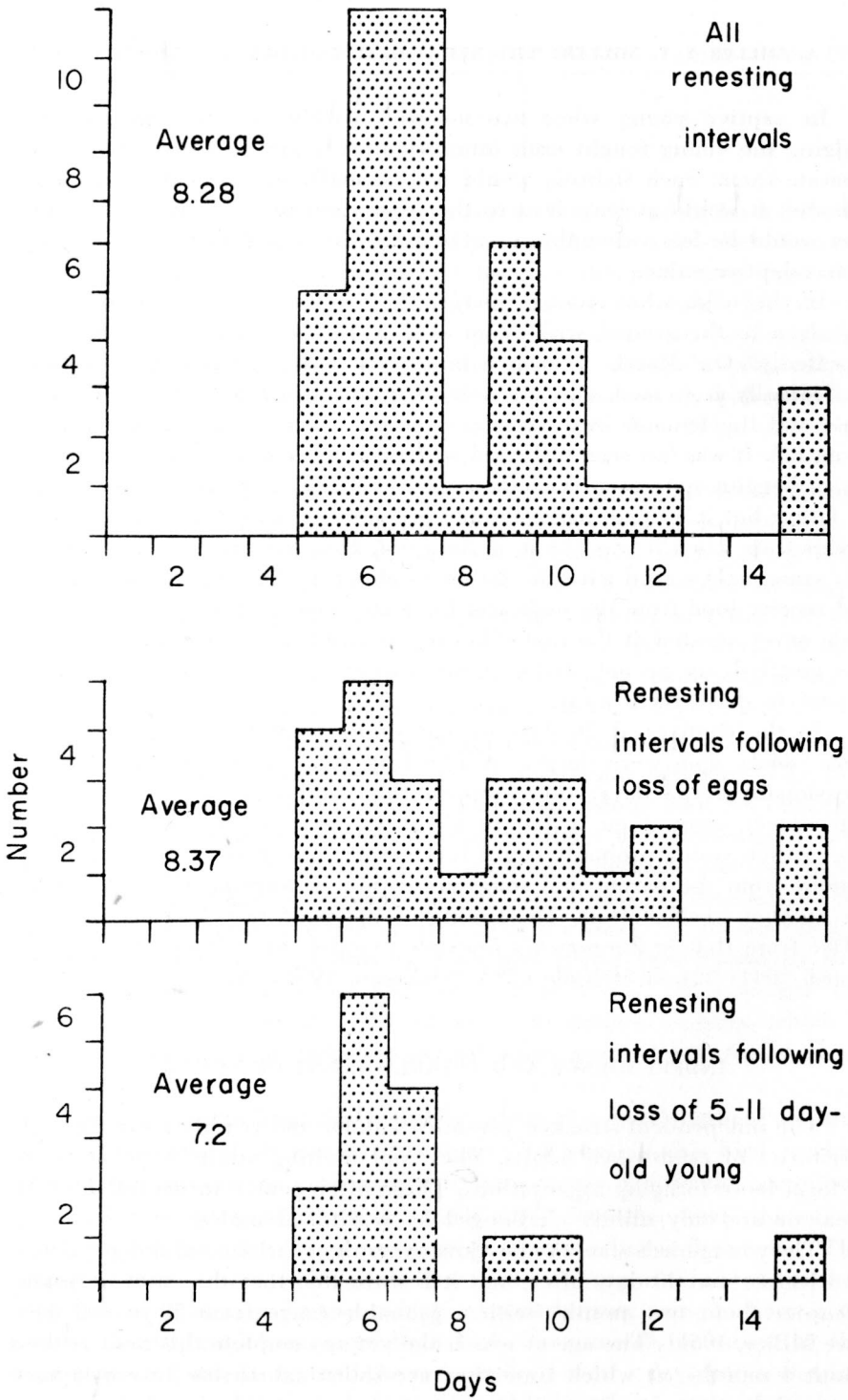


Fig. 12. Renesting intervals for captive *Zonotrichia capensis* showing trend toward shorter intervals following loss of well-developed young contrasted with loss of eggs.

Earlier, evidence was presented (Miller, 1959) to show that young males (7 cases) reach breeding condition at 5 to 11 months of age in the wild and two cases were recorded of females that had laid their first eggs at estimated ages of 4 ½ and 9 ½ months. Two cage-reared females laid their first eggs at 7 ½ and 9 months but this interval involved a winter short-day period (see Miller, 1965) which may have delayed these first nesting efforts.

At the early first reproductive periods the skull closure has not been completed but the residual immature areas are reduced to a fronto-parietal spot on either side of the midline that is usually no more than 2 mm. across. The remnant of such immature spots among wild birds of known age is best represented in juvenile 481 which was followed through to maturity. It had immature "windows" 4 mm. wide at 4 months, 2 ½ mm. wide at 7 months, 2 mm. wide at 9 months and none at 11 months. Another bird, no. 467, at 6 months had a 2 mm. spot and at 7 months this had reduced to 1 mm. Still another, no. 831, had a 1 ½ mm. spot at 10 months. Two others at 11 months had a mere trace of a spot and none, respectively.

REPLACEMENT NESTS

If a nest with eggs or small young is lost, females recycle readily. As already described this took place in female 485 in 7 days with the first laying 7 days following the loss of the preceding fresh eggs. In the captive colony, females were allowed to keep their eggs to the end or a little beyond the normal incubation interval if they failed to hatch. Females would usually sit on infertile eggs for 3 or 4 days past hatching time. For those hatching, the young were usually left in the nest to ages of 4 to 7 days.

In the captive colony 43 recorded cases of replacement nests had sufficient detail to fix the interval from loss of eggs or young to the time of the laying of the first subsequent egg. The interval, as shown in fig. 12 ranged from 5 to 15 with the modes at 6 and 7 days and an average of 8.28 days. Separation of these records by females showed no statistically significant differences, although the oldest female, when she was of a minimum age of 5 to 7 years, appeared to be showing a longer average interval than the young females that were 2 to 4 years old.

The renesting intervals when grouped according to the stage in which the preceding effort failed showed a suggestive trend (fig. 12). There were 24 cases in which renesting followed loss of eggs, chiefly loss for failure to hatch, after 12 to 15 days in incubation. These may be contrasted with 15 cases of renesting following removal or death of young 5 to 11

days old-young which were no longer at the daytime brooding stage. The renesting following egg loss averaged 8.37 days and that following late-nestling loss averaged 7.2 days. These differences fall short of statistical significance but the trend may have some biological meaning. One might have assumed that in birds that had carried the first nesting through far toward completion the urge to nest or the sequence of instinctive acts would have been more fully satisfied and a long interval would ensue before nesting again. The trend suggests at least that this is not the case and that any loss short of completion of the cycle immediately triggers recycling, perhaps even more rapidly if the time since the earlier laying is greater. It is also clear that the loss of either eggs or nestlings or perhaps just the emptying of the nest is sufficient stimulus to start a new cycle of ovulation in the female. It makes no difference whether she has passed the active brood patch stage and the daytime brooding regimen or not.

SECOND NESTINGS

It is often difficult to determine that nestings under field conditions are second efforts following an earlier successful nest rather than a replacement nesting. We gained evidence that second nests occur in the same reproductive season of some females, whereas they do not in other females.

For example, female 485 had a juvenile in attendance up to July 14, the young one though crippled being sustained through the full dependency period of about 33 days. Following this by 15 days, she was found to have a new nest with two of her eggs and one of a cowbird. The second nesting interval must have been in the range of 6 to 14 days. No molt or reproductive rest period intervened.

Female 487 on June 23 was seen with food near a dependent juvenile. On July 23 a second nest was found, the exact interval from the preceding effort was not determined, but clearly it was somewhat less than a month, and no molt had intervened.

Female 494 on July 19 had a juvenile following it, and it had been seen feeding such a juvenile two days before. On the 19th this female was seen carrying nest material. Whether she carried through with this second nest or not could not be determined, but at least it showed evidence of starting a second nesting as its preceding young reached independence.

On the contrary, we know that the two mates of male 460 raised one young each to independence in nestings dating from layings of about February 1 and June 8 following each of which the adults molted and did not second nest. They nested again after the second molt in the

following January, whether or not successfully to the point of juvenile independence could not be determined.

The history of female 483 is also instructive. This bird had an active brood patch on April 19 following a general molt in February and March and she had fairly advanced young from this nesting effort on May 8, although the size of the young is not known. On May 29 she again had an active brood patch. This could have been a second nesting although she was not seen with prior young approaching independence. She again had an active brood patch on June 28, representing probably a renesting. On July 14 the brood patch was starting to refeather but this general molt activity was arrested and she again had an active brood patch on July 28. She then molted completely in August and September and subsequently had active brood patches on October 3 and December 31. This female did not generally have much success with her nesting efforts and we had no success in finding her nests to follow their progress. However, she evidently had several repeat nests and/or second nestings in two breeding periods from at least April to late July and from early October to January, separated by a two-month nonbreeding and molt period. Several other females have records of two breeding periods each with one or more nesting efforts in the course of the year and with complete molt and non-nesting periods intervening; their histories are not as fully recorded as that of female 483.

PAIR RELATIONS

Adults and late immatures which have established territories are normally found in pairs and we found no cases of polygamy. The paired relation persists from one period of nesting to another. Much of the time when the birds are not occupied with nest duties or the male is signing, the members of the pair are in sight of one another or in touch through use of the soft pair association note. In some pairs, the moving about together is much more in evidence than in others, and in a few cases, as in that of male 466 and female 485, the birds, although in the same small territorial area, rarely were close together and then chiefly during the pre-laying period.

The relationships between 460 and 488, the latter the second mate of male 460, were more typical. In late April and early May, for example, when they were not nesting, male 460 was in the late stages of molt whereas female 488 had finished her molt at least a month earlier; the pair was then watched for several long periods. For example, on April 29 for an hour in mid-morning, there was no singing but the birds moved together along fences and through bushes, the male usually following

the female and occasionally taking a guarding position on a lookout post. The female ate a moth and one or both birds gave the pair association *sep* every few minutes. In this period, on open ground or in the grass, the members of the pair would forage within 1 to 10 feet of one another. On May 3, the male left the female to drive out another bird along the east boundary of the territory and he engaged in two different song bouts. This pair was not yet building a nest. In fact, it did not do so until the first week of June. This was then a non-nesting period, although the male was in reproductive capacity at least by May 3.

In another pair, the two birds were moving about, often as close as 6 inches to one another, silently, on October 2, following a period in September when the male was regressed (testes 2.6 mm. long, September 8) and before the cloaca had shown signs of recrudescence (October 20).

In such established pairs, then, the pair bond may be very real through a non-breeding interval or when the reproductive cycles of the members are not synchronized and one is not reproductively capable. At such times and also in a nesting period, song is infrequent when the birds are close to one another. Territorial defense occurs, however, and the female as well as the area are guarded. Song is most conspicuous when the female is on the nest and it often starts just after she has gone to it. It is heaviest in unmated, usually young males in the course of territorial and pair establishment. But it should be stressed that individual variation in song and in pair interest is great. For example, in captivity two pairs that have repeatedly nested, and with about equal success, show some definite contrasts. One male sings at least three times as much as the other (they are in adjoining cages but screened from view of one another) and the pair with the more vocal male more often moves about in close association than do the members of the other pair, which often fight. Yet both these males feed young in the nest.

PAIR FORMATION

The history of two young males is instructive in showing establishment in an area and attraction of mates. Male 491 at an age of about 9 ½ months on September 18 began singing vigorously in a small area previously defended for a few days time by another young male, which he displaced and which moved 30 feet away. For 14 days we could detect no female associated with male 491 in his newly possessed and rather small area interdigitated between territories of old males. On the 15th day he was seen with a female, no. 837, known to be young, and a pair association evidently was formed. Ten days later the female was seen carrying nest material and the male was close beside her. After the date of pairing,

he sang frequently but not steadily as before; he often remained silent for long periods or, when close to the female, he gave the pair association notes.

On December 2 male 491 had disappeared (he was never seen again), although he had been seen a few days before, and male 486 had taken his place in the area, the latter a young male of about the same age. Male 486 sang abundantly on this date and was seen near the female of 491. On the next day she was seen tolerating him at a distance of six inches on a feeding tray in the territory, although she made a slight threat move toward him. He moved toward her frequently, strutting with tail spread and wings drooped; they evidently were new acquaintances not fully adjusted as mates. His song began to diminish in the subsequent few days and the pair seemed then to be on a normal basis.

PAIR CONSTANCY

Early in the year that was spent at our field station the territorial males in the vicinity of the house were color banded. By March, 2, 3 weeks after arrival 11 males were thus marked and their song posts and at least part of their territories in which they were dominant were evident to us. The original eleven males may not all have been adult in February in the sense of having full skull closure and being 10 to 12 months old, but each was in or concluding an active breeding period and was in full control of an area. Each of these 11 males survived the year, having been verified as still present on its territory well into the following January.

The foregoing rather amazing survival of the territorial males was not equalled by the females that were their mates, although most of these also survived. The clear determination of pair association in some cases was not possible at once, but the males were seen with no other females and the females had been trapped and marked in February in the same area; therefore, pair constancy from February on was highly probable. Table 3 shows the 7 males that retained the same females through the year and the number of separate breeding seasons of the pair through which the pair relation was known to have been maintained.

The history of the other four established males represents cases of replaced females, two of which were due to separation of the pair and not death or unexplained loss of the female:

(a). Male 480 was seen paired with female 487 in August. She was an old female that may have been with this male when both were captured in February. Female 487 was incubating in early August and then disappeared, never to be seen again. Male 480 was mated with 832 in the January following; this female then was about 12 months old.

(b). Male 472 was mated with female 462 in April and May. She was last seen on May 25. In November and December 472 was mated with female 840, a young bird about 10 months old.

(c). Male 475 was mated with female 493 from March through May at least. But in July she was going with no. 824, a 7-month old male while male 475 was now mated to female 844, a bird at least a year old; he then nested with 844 in two successive breeding periods. This then was a case of divorce and remating after the May nesting of male 475, who remained in control of the same territory throughout.

(d). Male 460 was mated with female 462 in February and they successfully raised a juvenile. She went into molt earlier than he and by April 18 was the mate of 472 in an adjoining territory, remaining with him at least through May. Male 460 in the meantime was joined by 488, an old female, on April 28, and they remained paired the rest of the year through two successful nesting seasons. This was again clearly a case of divorce and remating among territorial neighbors, the males staying in fixed position on their established domains.

The young male that successively held a territory beginning in September (p. 132) had formed a pair relationship with female 837 and it was she that remained on the area when her first mate disappeared and a second male took its place and paired with her.

COURTSHIP AND COPULATION

The establishment of the pair evidently involves approaches to the female by the male in the form of strutting with tail fanning (see p. 98) and this type of display along with singing may be regarded as a phase of courtship. However, no attempts at copulation follow this early demonstrating. Courtship that might stimulate or precede copulation when nest construction and egg laying is underway would seem to entail again considerable strutting by the male who rarely engages in this toward the female in the pre-nesting intervals.

On May 12 a female was gathering nest material and the male once flew to a fence wire 3 feet above her and widely fanned his tail and crouched, rather than strutting in erect posture.

On December 14 a female that at least two days later had a new brood patch was approached by the male. He flew down to her, a chatter rather than a defense screech ensued, but there was no immediate copulation.

In captivity in the period just before eggs are laid, males were several times seen to grab in their bills the rump feathers of their females

and hang on in what seemed to have been ineffectual attempts to copulate; under these conditions the females screeched and eventually struggled free and no mounting ensued. Such approaches by males seemed in several instances to follow upon alarm to the caged birds occasioned by our presence, as though the action were a displacement behavior during the period when mating interest or urge was great. Blanchard (1941: 24) describes similar "attacks" in wild *Zonotrichia leucophrys* and does not regard this as either sexual fighting or pouncing as reported in reed buntings (Howard, 1929) or song sparrows (Nice, 1937: 84), an interpretation with which we agree. Blanchard (1941: 24) discarded the idea that these attacks resulted from the female's lack of receptiveness to copulate. Our view of this in *leucophrys* and *capensis* is that the attack results from some lack of synchrony in the approach to copulation by the members of the pair. This could occur even though both are sexually active, as we know the males of *capensis* to have been, and in the same period of days when successful copulation does occur. Such attacks are different from frontal approaches or fights between males or between members of a pair that jab at each other with their bills and clutch or cling with their feet.

An example of this "copulatory attack" was noted on May 31 when we approached a captive pair. The male stopped singing and flew to the female at once and seized her rump feathers. She screeched loudly and tried to get away. The male gave a full, but somewhat subdued, song while still hanging on with his bill; he then let go. On another occasion this male hung onto the rump of the female while they flew.

In another instance when possible copulation occurred, a male in a cage flew to his female who was on the ground picking up nest material. He seized the feathers on her rump and the two moved forward in a waddling walk, disappearing from view behind cover. There was no screeching and two seconds later the female reappeared and fanned and closed her tail several times. The male flew up to the screen above and sang vigorously.

The one certain case of copulation witnessed was in a caged pair, four days before egg laying. The pair came out of the shelter and mounted without any sound or preliminary posturing. Both birds remained silent but rapidly flapped their wings during the copulation, which lasted about 11 seconds and took place on the ground. The male then hopped off over the head of the female and flew off a short distance.

The female invitational display described earlier (p. 98) may not then precede copulation, or perhaps is not required immediately before. Yet this action, with the warble, crouching, and tail fluttering, clearly is the stimulatory or invitational behavior of the female as seen in other

sparrows and we saw it in captives and in the field only in the 10 days preceding a laying. For example, female 485 on November 30 three times warbled and one time accompanied it with fluttering wings, crouch, and elevated tail, while the male sang on a perch above. Although no copulation was witnessed, she laid three days later.

TERRITORIAL BEHAVIOR

The territorial behavior in *Zonotrichia capensis* conforms fairly closely to the classical pattern in which the home area is defended against other adults of the species so that there is effective exclusion of them from it. The male, using song at a distance, and threat and actual fighting at close range, is the defender of the area, exerting dominance over other adult males that approach or invade and himself becoming subordinate in the area of another male, or in some neutral areas outside his territory being rather non-aggressive or ambivalent toward other individuals.

The differences in territorial behavior from the classical pattern arises for the most part from the lack of synchronized seasonal events in the population and in the continuous possession and defense during the life time of the individual male.

Other features of the territories of *capensis* are the tendency, sometimes well marked, of the female to disregard the boundaries and to pass through several territories unaccompanied by her mate in the course of foraging missions. In such crossing to and from neutral areas, females were often challenged but at other times pass through quickly, seemingly unnoticed. The territories, as determined at our station, were so small that the males could survey the whole protected or dominated areas from their song posts or any elevated spot in them, and they did not range about in a patrolling movement.

SIZE AND TERRITORY USE

The approximate boundaries of twelve territories grouped about our immediate house and gardens as of December, 1958, are shown in fig. 13. Each is designated by the number of the male in possession and all areas had been occupied by these same males since the preceding February except for that of 486 which was established later by young males in mid-year (see p. 127). The east side of the main road shown was uncut forest and unsuited for zonotrichias except at the disturbed border. To the west and east of 480 were open areas of low or heavily grazed

pasture that were too open to provide cover for permanent occupancy by zonotrichias. To the south and north of the plot were other similar sparrow territories which were, however, too incompletely studied to permit mapping. On the east and southeast sides of the house, in open flower gardens and walkways and at the front doorstep, were feeding areas not controlled by any male; these were essentially neutral zones. So also was an area where garden trash accumulated west of territory 466 by the servants' house. The front doorstep was especially visited, for a night light over it attracted great numbers of moths that in dead or dying condition were fed upon by the sparrows each morning throughout the year. Much trapping was carried out in these neutral feeding areas and birds from immediately adjoining territories and those from two territories removed would show up in them.

Each territory had at least small trees, bushes, or fences for song and lookout posts and some dense bushes for roosting and nesting cover. All also had some grassy patches or more or less bare border paths used in ground foraging.

These territories usually had a greatest dimension of about 100 feet and a least dimension of 60 to 80 feet. The area was thus usually about 7000 square feet or about a sixth of an acre. This is surprisingly small, substantially smaller than in wren-tits (Erickson, 1938) but not different from those of resident salt-marsh song sparrows (Johnston, 1956: 255).

Because of the small size and use of extraterritorial feeding areas, one might surmise that the established pairs do not depend on their areas extensively for food but use them principally for nesting. This is not the case, however. Although we have no good data on the amount of time spent in the territory, it was evident that most of the day the pair was in its territory foraging or loafing and that occasional foraging outside, perhaps no more than two or three times a day, took them to especially attractive feeding sources. For hours at a time a pair that was engaged in feeding young would be seen foraging inside their defended area.

Examples of movement to points outside the territory are as follows: male 484 could be found at any time he was looked for diligently over a period of a half hour or less in his territory south of that of male 460. He never sang anywhere else. He was seen and his identity checked 61 times on 54 different dates over an 11-month period. On 23 of these occasions he was seen about our house at food sources, but since we had a much better chance of seeing him there, where we were present much of the time, this type of occurrence outside the territory should probably be reduced by a factor of 5 to 10 and might thus be only 3 to 6 per cent of the time. The occurrences away from home tended to concentrate in the periods from late March to early May and from late

July to September, both periods when he was not nesting but was molting. However, in these periods he still was attached to his territory and could be seen on lookouts chipping or occasionally singing. In leaving his territory he had either to cross or move around that of male 460. Whatever the route, he showed up at our front steps, the north court, and at the west or back door.

Another pair of birds that was instructive in the matter or ranging from the territory was male 482 and female 483. She was regularly seen with her mate on their territory but she came often across the territories of 475 or 460 to the house and gardens, turning up in the traps repeatedly and becoming thoroughly habituated to them. She would repeat two and three times a day and was recaptured a total of 47 times, all but two of which were at the house away from her territory. By contrast her mate was detected at the house away from the territory on only 3 occasions in the course of the year, and then not in her company.

The greatest distance of movement of a pair was that of male 491 (predecessor of 486) and his mate female 837. On October 6 in late morning they were seen in a cow pasture 150 yards from their territory, moving together but mixed with a loose aggregation of foraging zonotrichias and grassquits. A half hour later they were back on their territory where the male had also been singing earlier in the morning.

TERRITORIAL BOUNDARIES AND DEFENSE

The mapped areas (fig. 13) of necessity show fixed boundaries. As in many territorial systems, however, these are variously rigid. In *Zonotrichia capensis* the boundaries between adjacent males were often well marked and were tested or fought over repeatedly. Such was true of the border between 460 and 475 in the front garden. This line had a fixity along an upper terrace that was definable to an accuracy of a foot or two, but on other parts of the periphery of a territory, there might be no competing male and the area habitually used and guarded had only approximate limits which seemed at times to fluctuate by 10 to 30 feet. The areas shown then were in no sense all rigorously held throughout with proven, defended boundaries. They were however the regularly occupied areas of dominance.

A male guards its area by taking exposed perches and singing from them in varying amounts. Use of song varies with the individual and with the breeding activity. Both during nesting periods and otherwise, invading adults are flown at and chased with defense screeches sounding as the birds come close together. Following a chase or challenge the male in

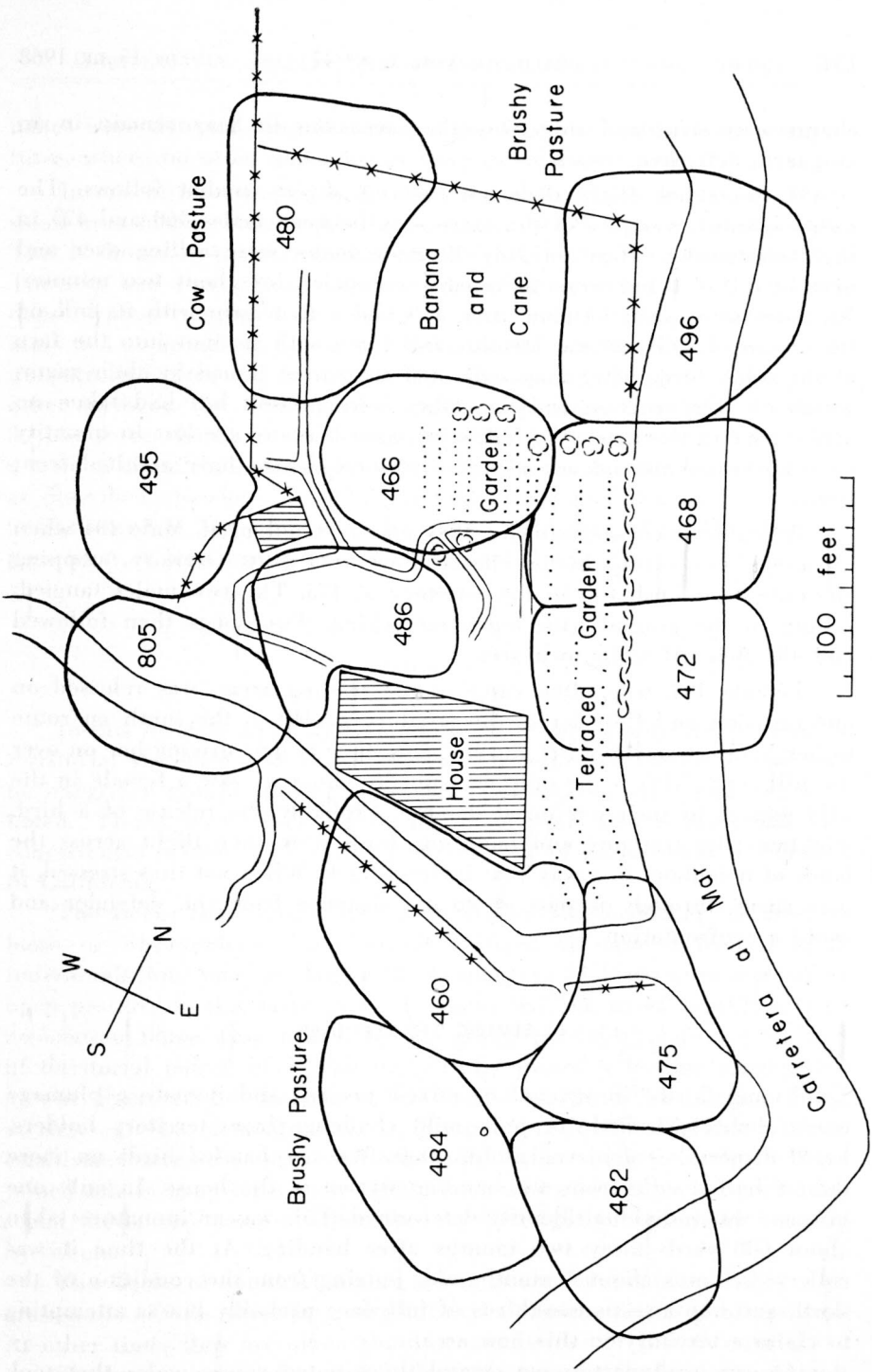


Fig. 13. Map of territories of *Zonotrichia capensis* about the house and gardens at Santo Domingo as of December, 1958. Each territory is designated by the band number of the male in possession.

charge may strut and sing. On other occasions he may remain in an on-guard, defensive crouch.

If the attack flight does not succeed, direct combat follows. The most vigorous examples of this were seen between males 460 and 475 in the front garden. Here on July 20 these males were rolling over and over in the dirt and were thoroughly entangled for about two minutes. No notes were given. At one time 460 had a firm grip with its bill on the crown of 475 and was striking full force with its foot into the face of the other bird. After they separated they were joined by their mates which on this occasion and one other were present but had taken no active part in the battle. In fights in cages, feathers are lost in quantity on some occasions and we suspect that some deaths have resulted from fights.

When birds cross territories, they may be challenged. Male 484 when released from a trap by the house flew toward its territory, stopping en route on a bush top in the territory of 475. The two males tangled, falling to the ground with much screeching. Two songs then followed and 484 flew off to its own area.

Female 483, who often came to the feeding areas, was released on one occasion and flew across the territory of 460 to the south en route to her home area. Both 460 and his mate flew at her, driving her on over the hill crest. This is the only occasion in which we saw a female in the wild engage in such territorial defense. Probably the release of a bird, frightened by trapping and handling, leads it to take flight across the lands of neighbors in a way that invites attack. When not thus stressed, it may sneak through or pass at greater distance from the defender and avoid a confrontation.

CLAIMING TERRITORIES

Young birds in juvenal or mixed juvenal and immature plumage move about with little or only mild challenge from territory holders. Local dispersal is achieved at his stage. We saw banded birds no more than a half a mile from our banding station at the house. In only one instance was individual identity determined. This was an immature taken about 600 yards away two months after banding. At the time it was collected, it was about 6 months old, judging from the condition of the skull, and had a testis two-thirds of full size; probably it was attempting to claim a territory in this new area.

At our headquarters we several times noted young males that took up song posts and began singing vigorously and almost continually. No

mates were detected, and the areas were marginal, rather too-open pastures, where no other zonotrichias were established.

In one instance young males did succeed in setting up a new, rather small area north of the house between areas held by established adults. This is shown on the map as belonging to male 486, the ultimate holder. The area had a steep grassy slope, a section of bare yard, and three small dense cypress trees used for song posts and potentially useful for nesting. Male 493 at an age of about 9 months started singing in this previously uncontrolled area on September 10. He was aggressively driving out other birds on the 13th. By the 18th he had moved or been displaced 30 feet to the north into a neutral area and his place was taken by 491, a male of about the same age. Nº 491 attracted a mate (837) on October 3, as described elsewhere (p. 132), and his control of the area continued until the end of November when he was in turn replaced by 486 who held possession at least until our departure on January 21.

FLOCKING

In this resident equatorial population of *capensis* with the permanent territorial structure just described, the formation of flocks is rare and no integrated groups, moving or travelling or seeking cover together were noted. There is in such aggregations as were seen nothing like the cohesiveness evident in Winter visitant flocks of *Zonotrichia leucophrys* in California.

The flocks that were observed were always recorded at the time as loose or disorganized. They usually ranged in number from 3 to 12 individuals, but once, on August 28, as many as 25 birds were seen in an open pasture. In this large group frequent fighting notes as well as pair association notes were heard, so the group probably consisted in part of territorial paired birds that had briefly joined a feeding aggregation as was described for the pair 491-837 on October 6. Thus flocks consist at times of two elements, namely, juvenal and immature birds without established territories and territorial adults that singly or as pairs have joined others away from their territories under a weak, partly conflicting social drive, and possibly stimulated by the sight of successful foraging by others.

The flocks of zonotrichias are often in association temporarily with grasssquits *(Tiaris olivacea)* and goldfinches *(Spinus psaltria)* in pastures. At other times they are alone about accumulations of garden debris.

Flocks are more often than otherwise seen in the periods of molt and infrequent nesting and reduced singing. Thus we noted specifically

that flocks were seen on 6 occasions from July 25 to October 21 and on 3 occasions from February 23 to April 16. These of course are the times when most young birds are present, the product of the preceding periods of augmented breeding, and it is also the period when territorial holders seem usually to be somewhat less aggressive. In the principal breeding period of December we twice saw 3 or 4 birds together feeding, but only briefly, the apparent association soon breaking up or a fight ensuing.

SEASONAL AND DAILY SONG CYCLES

Inasmuch as some zonotrichias are breeding at all times of the year and song is used or stimulated by a variety of situations and is subject to much individual variability, song seasons are very poorly defined. We could not quantify song in the population in any meaningful way. During a period of infrequent song, an occasional young male might start to establish a territory and sing heavily (p. 134), sometimes stimulating other birds that generally were quiet. On other occasions a clearing of the sky following a rain would seemingly stimulate singing in a group of territory holders that had been rather quiet and there would then be a flurry of singing, one bird rather evidently stimulating song in neighboring birds.

One nonetheless gained a clear impression that song was scarce or even absent on some mornings in the molt periods (Miller, 1961) and that it was abundant during the two peaks of nesting.

The daily song performance starts with songs delivered from the night roost. As in related sparrows an occasional song heard earlier than others may not represent the real dawn song period, in which for a brief time song is regular and engaged in by many individuals. The timing of the dawn song period was not often ascertained and was difficult to relate to sunrise and light conditions, for fog prevailed at sunrise on most mornings and sun position could not be determined. Also the density of the fog was variable, so that a light fog might not delay the morning chorus whereas a heavy fog or rain certainly did.

As shown in table 4, records for dawn singing were made when the sky was entirely clear on two mornings. On the other occasions there was only light or broken fog. The variability in time is only imperfectly related to the slight seasonal change in photoperiod and sunrise, which would fluctuate about 20 minutes from the slightly shorter days of February to the longer days of June. Estimating of sunrise, both from observation and sunrise tables, shows that throughout the year these song times fall 15 to 20 minutes before sunrise on clear and lightly foggy

mornings. On the morning of April 13, when the sky was clear, light readings were attempted and it was found that the first possible reading with our instruments was ½ foot candle at 5:48, 12 minutes after the start of the dawn chorus.

The dawn singing usually begins to diminish about 18 minutes after its start, presumably as the males then move to the ground to forage where light readings were checked and found to be 6 foot candles.

Song continues in the morning in variable amounts and with different individuals participating. In mid-day, especially in a sunny warm period, it is infrequent. An evening song period is not conspicuous, although some increase in song in late afternoon is evident. Singing as the birds go to roost is erratic. Certainly there is not a regular chorus, then, and on evenings of heavy fogs, which was the rule, there was no song at the time of sunset. More often the last sounds heard from the birds were the anxiety chips. For example on April 19, the last foraging was seen at 6:21 with light at 4 foot candles, and no chips or songs followed. At 6:24 we registered 1 foot candle and this was about 15 minutes after sunset. But on June 25 at 6:35 we heard late songs and calls on a clear evening; this was about 20 minutes after sunset.

These data indicate a period of daily wakefulness of 12 ½ to 13 hours, according to the time of year but part of this at either end is while the bird is on the roost so that only about 12 ¼ to 12 ¾ hours of full activity with the possibility of foraging is available during a daily cycle of a male. A similar "working" day was recorded for an incubating female in December.

FOOD AND FORAGING

As in related emberizine sparrows, adult *capensis* are predominantly seed eaters whereas the species feeds insects to its young. We did not make stomach analyses and cannot estimate closely the proportion of seeds, other vegetable material, and insects in the diet of adults.

Andean sparrows obviously depend a great deal on grass seeds, green or dry, taken from or among the plants and gleaned from relatively bare ground and litter near plants. They hop or skip-hop through grass 3 inches tall and also work through higher grass and bushes but do not drop down into grass stands 2 or 3 feet in height except along paths or in places when the grass is broken down, nor do they cling to tall grass stems in foraging. Their preference for seeds is shown by their attraction to bait of canary seed, rolled oats, and cracked corn. They were the only birds in the area of our station thus attracted significantly to such bait.

We have seen them tugging at grass in seed, which is present throughout the year, and also have noted their scratching in litter of leaves and stems apparently to expose seeds and insects. In captivity birds can be kept in healthy condition for long times on nothing but canary seed.

When young are being fed, insects are gathered chiefly from near the ground but also on wall surfaces and in low bushes. Moths were identifiable repeatedly in the beaten and dangling insect masses that the parents carried to their young. At Santo Domingo, as mentioned earlier, the night lights drew a year-around supply of moths that were available each morning on the steps and walls. These were gathered and the wings beaten off and crushed; such sources of food were used regularly by several nesting birds with territories near the house. But we saw other adults obtain moths in the garden, and captive birds chased them when they came into the cages. In our efforts to raise captive young we found that adults would readily take aphids from plant stems, small grasshoppers and crickets, and wax-moth larvae and feed them to the young. Meal worms were eaten but we avoided using them for small young. Fly larvae and dried flies did not seen attractive to the adults.

During nesting periods at least, adults themselves eat some moths and lepidopterous larvae. We once saw an adult feeding on a banana on the ground, but fruit generally was not sought and did not particularly attract them at feeding stations and traps.

Because of the seemingly constant supply of grass seeds and of insects at our station, we could not detect any seasonal variation in food availability. Fluctuations in food supply of a subtle type cannot be ruled out but extensive sampling and analysis would be necessary to demonstrate it. We think any large fluctuations would have been evident to us.

BROOD PARASITISM AND PREDATION

Cowbird parasitism.—Already reported (Miller, 1963: 47-48) are details learned of the parasitism of nests of *Zonotrichia capensis* by the cowbird *Molothrus bonariensis.* At Santo Domingo we saw 3 cases of successful parasitism leading to the fledging or independence of the cowbird. In these cases there was no sign that the zonotrichias raised their own young. This is not surprising since they seldom raise more than one young from a nest anyway.

The two nests seen with cowbird eggs each had the usual two zonotrichia eggs also. No zonotrichia eggs may be presumed to have been removed by the cowbird therefore. Nestling or fledgling competition apparently does away with the young zonotrichias.

Parasitism occurred chiefly during the period from February to July, and it would appear to have its greatest impact on the sparrows in their peak nesting of May to July but not in their other peak period of November to January.

In the Santo Domingo area cowbirds are not common. There may be only one laying female in an area of 25 or more sparrow territories and such a female may lay 3 to 5 eggs one or more times in a breeding period. The impact on the productivity of the zonotrichias cannot be quantified. It is not a large factor, yet it is by no means negligible. Certainly female 485, the only banded zonotrichia to raise a cowbird fledged in the year, raised but three young of her own rather than four as a consequence of her contribution to the cowbird population.

Predation.—Direct evidence on predation is virtually non-existent as is so often true in observing a wild population of birds. Some inferences and probabilities may be stated, however.

At the nest and egg stage we believe that losses to rodents and snakes are likely. A small colubrid snake *(Leimadophis pseudocobella)* and a large green colubrid *(Chironius carinatus)* were species occasionally seen in the garden and in the pastures. Also among rodents *Rattus rattus* and two species of *Oryzomys* were present, the latter rather commonly along the pasture borders. In cages at Berkeley white-footed mice *(Peromyscus truei)* took eggs from nests on several occasions and one may presume that *Rattus* and *Oryzomys* would do so when they came upon nests near or at ground level. Opossums *(Didelphis marsupialis)* present at our station likewise were potential nest predators. We found two nests with eggs destroyed by the cutting over of pasture lots by man; probably this happens rather often.

Young in the nest and in the post-fledging period, when they live in the dense bush cover, would appear to be vulnerable to the aforementioned snakes and to opossums, large rats, and to weasels *(Mustela frenata)*, one of which was seen in our yard, and to the tayra *(Tayra barbara)* which was seen in the forest edge. We suspect that smooth-billed anis *(Crotophaga ani)* also take such young, as we saw one attack an adult caught in a net, and adult sparrows are alarmed by the presence of anis near their nests and young.

Experienced adult birds are probably not particularly threatened by anis, opossums, or rats, but they presumably are preyed on by hawks as one may infer from their special song alert (p. 92) given when hawks are seen. At Santo Domingo the principal hawk predator is *Buteo magnirostris.* Weasels and tayras are active enough to threaten adults, and females on their nests may be lost to snakes, as happened once in captivity. We had one report of a boy killing one of our banded birds with a sling

shot and we saw several unsuccessful attempts at this. Probably dogs capture an occasional sparrow.

SURVIVAL AND RECRUITMENT

The size of the population of sparrows at Santo Domingo was canstant through the year. As shown earlier (p. 134) the number of male territory holders did not vary significantly and individuals remained attached to their areas to form a very stable population structure. The non-territorial immatures did not fluctuate importantly in the area as shown by weekly surveillance and by trap recapture records. There was a noticeable increase in juveniles following each of the breeding peaks but these diminished in a month or two either through dispersal of failure to survive.

By the end of the first month of trapping most of the adults within two or three territory units of the house had been color banded as had also most of the current crop of young birds that had been produced nearby. Occasional new adults (11) that came in to feed from farther away were caught from mid-March to May 2, but after that only three new adults were taken —one each in June, September, and October— for the remainder of the year until our departure in late January of 1959. The later-detected adults in only one instance took a place among the territory structure close about the station grounds. The others were either never seen again, apparently because our traps were beyond their usual extra-territorial foraging range, or they appeared only once again at the traps. We observed about half of them at one time or another stationed in areas west and north of our grounds beyond the plot of mapped territories.

These circumstances indicate that the adults caught and marked in the first 3 weeks from February 10 to March 2 represent the virtually complete set of territory holders in the areas that could be watched thoroughly and that could be retrapped with some frequency. This territorial population consisted either of adults or birds at least old enough (6 months) to be engaged in their first nesting effort, but for estimating survival through the year the group will be referred to as the adult or mature established population.

As shown in table 5 the initial adult population of 31 showed high survival in the course of the year. Twenty-two or 71 per cent survived the entire year through or into two nesting-peak seasons subsequent to the one in which they were captured. The drop out of the 9 birds is rather evenly spread through the year, suggesting a steady low rate of

attrition. Of course we do not know the cause of their disappearance. Some may have moved away and yet survived, for cases of pair separations (p. 127) have been detected. Probably most do represent mortality.

The young birds with which the record year started consisted of 30 juveniles or birds in the postjuvenal molt that initially were captured in the month of February 14 to March 15. This group shows a survival to the end of the year of 4 birds or 13 per cent and an interesting drop-out record. The heaviest loss was in the first two subsequent months, and from month 3 to 9 there was a slow drop-out rate similar to that in adults. The losses or disappearance, of course, must represent dispersal in considerable degree, for these young are non-territorial and in general moving about to find new areas for establishment or to replace gaps in the adult territorial group wherever they occur.

Of particular significance is the fact that the four young birds that we proved survived the year filled in the gaps in the local group of adults. The other birds that settled locally and gradually filled the rest of the deficit in local adult birds consisted of one known adult and five immatures. These latter five immatures were not among the young banded in the first month. They may be regarded as in part representing inflow from surrounding areas of production, balancing outflow of young from the local area, and in part later-produced young.

In any event, we were able to witness, in effect, a replacement of the adult territorial population by immatures, about half of which were produced very close by, if not on the actual territories under consideration. If we view this replacement group as the total survival of immatures out of the original 32, since emigrants should balance immigrants, we estimate a survival of young post-dependency birds as 30 per cent. Conversely there is a 70 per cent loss among such young over a period of their first year. But more than half of this loss evidently takes place in the first 3 months of that year.

The survival and loss in the population when separated by sexes does not reveal a dependable difference. Survival in males tends to be somewhat higher than in females, but larger samples would be needed to establish this. The territorial males were somewhat more readily observed than the females, althongh the situation in the 12 territories thoroughly studied would not have been affected by this difference in observability. But females in areas farther away might have been missed more often than males and their survival therefore might have been a little higher than the figures suggest.

If one assumes that the record of survival and recruitment at Santo Domingo in 1958 is fairly representative for the species in such an environment and that roughly a 30 per cent replacement is required

for a stable population, each pair must on the average bring to the stage of independence about two young a year in view of the losses subsequent to independence which are indicated.

Since rarely does more than one young reach the late dependency stage from a given nesting, the adults should in each of their two nesting periods renest until at least one young is brought to independence. In view of the limited success in raising more than one young per nest there is no selective advantage to a clutch larger than the normal two. Two and probably 3 young can readily be fed in the nest to the fledging stage, but predation or some limitation in parental care, and not limitation on food delivery, in the post-fledging stage is the chief barrier to greater productivity.

Inasmuch as the climatic regime and lack of seasonality pose no bars to nesting at any time, the selective advantage to the species lies in many repeat nestings and not in laying more eggs or in having more nestlings at a time which in this environment they doubtless could adequately feed. In this way the species maintains a dense population and doubtless if it were less dense, or unusual slack in it occurred, a greater survival of independent juveniles and postjuveniles would build it up. This group of immatures is the expendable reserve, seemingly held back in their success in establishment as adults in part at least by the territorial system into which they cannot enter, on favorable terrain, without replacing a lost adult or possibly, rarely, displacing an old or weakened adult.

Discussion.—The well supported view applicable in many species of temperate lititude birds that clutch size is limited by the inability of the parents to raise nestlings from a large clutch of vigor equal to those arising from smaller clutches (Lack, 1947), must be viewed differently in such a tropical latitude representative as *Zonotrichia capensis.* First, one must realize that the pressure to produce large clutches is reduced here because long breeding seasons and repeat nestings are possible. Second, the slow food delivery rate to young in the nest, occasioned by limited need of the small number of young, leaves the parents with much free time, a condition which we repeatedly observed. This time could have been used and food obtained for more nestlings so that availability of food does not in itself appear to be limiting factor on clutch size (Skutch, 1949). Third, the infrequent visits to the nest that contains nestlings may reduce the predation on nests, promoting better survival; it made the finding of nests more difficult for us. Loss is reduced by not putting all one's eggs (or young) in one basket. Although we are far from convinced that nest predation is high in this equatorial sparrow compared with that in its temperate-zone relatives, still the species is in a position to counteract such predation as it suffers in a different kind

of way. Fourth, if because of some innate limitations in behavior of early post-fledging young or in the parental protection of them, parents cannot bring more than one young through this predator-vulnerable period, avoidance of laying more eggs by the female at one time may have energy-saving factors of selective advantage. The total drain on her in producing strongly viable eggs in repeat nestings would be less. In captive females that are over worked in repeat nestings, hatchability of fertile eggs was observed to drop off.

To conclude, then, large clutches are unnecessary in order to maintain strong productivity where breeding seasons are long or continuous and replacement nestings feasible. Small clutches are not required by limitation on food delivery to the young, but they may have selective advantage in reducing nest predation and in reducing the energy drain on the female in producing eggs.

Fundamentally, population control arises not from any built-in limiting features of reproductive behavior or physiology, the selective pressure for which acting on individuals as it must, we find difficult (contra Wynne-Edwards, 1962: 19) to conceive. Rather, control is effected by the system of territorial behavior which restricts by areal exclusion the number of breeding adults that can settle in a region, remain vigorous, and reproduce.

SUMMARY

The behavioral ecology and breeding biology of a wild population of *Zonotrichia capensis* was studied in the Western Andes of Colombia for a period of one year. This equatorial representative of a widespread emberizine sparrow of Middle and South America shows attributes that reflect the species' response to the stable seasonal conditions of tropical latitudes. Supplemental information derived from captive sparrows maintained at Berkeley, California, is introduced.

The wild population of zonotrichias was color banded for individual recognition and was repeatedly retrapped. Observations were made on 234 days of the year on the 4-acre area under intensive study.

The birds were found to be strictly resident and to breed throughout the year. Individuals do not breed continually, however, but have a double annual cycle of reproductive capacity, nesting, and molt which is largely innate (Miller, 1959, 1961, 1962) although somewhat influenced by the two wet and two dry seasons of the area.

The species occupies mixed brush and grassland, thriving where original ecologic conditions have been disturbed. Food consists largely of seeds of grasses and forbs. Young are fed exclusively on insects, of which moths are a prominent element.

The vocal communications of *capensis* are homologous with but in no case identical to those of the North American species of *Zonotrichia*. They are compared particularly with the vocalizations of *Zonotrichia leucophrys*. *Zonotrichia capensis* was shown to have a special song given as an alert or warning in the presence of a predator. This is apparently a unique feature among such types of birds. The vocal communications are much more like those of congeneric relatives than they are like those of members of closely related generic groupings such as *Passerella*, *Melospiza*, and *Junco*.

The species has a distinctive juvenal plumage but no immature or subadult plumage that marks young birds as different from adults. Sexes are not clearly distinguishable by plumage but some average differences in combination with partial size differentiation and behavior probably afford the basis of sexual recognition by the sparrows themselves. The crest formed of long crown feathers is more developed than in related species and its elevation and depression appear to signal certain emotional conditions, a raised crest generally being coupled with aggressiveness and alert and uneasy states.

The nest is constructed by the female alone and is rapidly completed, in some instances in as little as three days. Nests are placed in low bushes and grass clumps or, less frequently (4 of 19 cases), on the ground. The structure lacks a special base platform of sticks, and the cup of grasses and leaves and stems grades into the finer lining material; hair is occasionally used in the lining.

The usual clutch of eggs in this equatorial population is 2; this number is usual also in captives of this population held at latitude 38ºN in Berkeley. Two young often fledge but rarely does more than one per nesting survive the first 10 days after nest-leaving. Clutch size is larger in races in temperate South America. Eggs normally are laid on successive days and daytime incubation begins with the laying of the second or last egg.

Incubation is performed solely by the female and she is not fed by the male either then or during courtship. Attentive periods in incubation ranged from 12 to 59 minutes in one well studied nest and daytime coverage of the eggs was 81 per cent. The recesses ranged from 2 to 12 minutes. Longer attentive periods were recorded in another individual. The nighttime coverage of the eggs was 11 hours and 44 minutes. The incubation period in wild birds and captives is 11 to 12 days.

The female broods the young extensively by day during the first 3 or 4 days after hatching. The males show much individual variation in attention to the young, some never going to the nest whereas others feed young even more often than the female. Similar wide variation

among males occurs in matters of close attendance upon the nest-building and incubating females and in amount of singing.

The feeding rate at nests is low, despite rapid development of the young. Rates per nest per hour in the morning ranged from 1 when the young were one day old to 6 at seven days of age when food demand in consequence of the size and growth rate of the young is greatest.

Growth rate and development is virtually the same as in *Zonotrichia leucophrys* as determined by Banks (1959), the greatest rate being at 3 or 4 days and the greatest actual increments being at 6 to 7 days of age. Weight reaches a plateau at near the adult level at 9 to 11 days. Fledging is at 10 to 12 days and is, if anything, later than in *Zonotrichia leucophrys* despite the smaller member of young and the similar physical development.

Fledged young stay concealed in the bush cover for about 10 days and then begin following the parentes in the open. Self-feeding becomes effective though not fully sustaining at about this time. Dependency on the parents for food wanes at 28 to 30 days of age but continues to some extent to about age 35 days. The age of independence is virtually the same as in *Zonotrichia leucophrys* in Alaska as reported by Oakeson (1954).

Young birds wander through territories of established adults, dispersing short distances only. At ages of 5 to 11 months they establish their own territories, or fill in for losses in adult pairs, and begin to nest.

Second nestings may occur in the course of a single reproductive period of an adult. Replacement nestings occur regularly, with new layings starting usually 6 or 7 days following loss of either eggs or young.

Established first-year and adult birds remain paired on territories throughout the year. No cases of polygamy were detected. Two instances of divorce were recorded. The reproductive state of the two members of a pair may not be coordinated in time over considerable intervals. Pairs are formed following heavy singing and strutting by the male; toleration at close range by the female then ensues and there is frequent use of pair association notes.

Territories, in which the male is dominant and excludes other males particularly, are small, usually only about 100 feet in diameter. Females to considerable extent, and males less so, range beyond their area to neutral feeding grounds, yet most of the foraging of the pair is done on the home area. Territorial defense is achieved by males by mounting guard posts, variously engaging in song, by chases, and by direct combat which may be very intense and lead to injury.

In the established population of color-marked adults survival was 71 per cent after a period of one year. Juveniles and immatures had a

calculated survival for a year of about 30 per cent. The total population level remained virtually constant with temporary peaks owing to production of young in the two principal nesting periods. Disappearance of young was greatest in the first 3 months after initial trapping, and the rate of drop-out then decreased to the same level as that for adults.

Recruitment of the population in a continuous-breeding population at equatorial latitudes is most efficiently achieved by small clutches of eggs and the many repeat nestings that are permissable under conditions of a relatively constant and abundant food supply. Small clutches are not required by limitations on food delivery to the young but they may have selective advantage in reducing nest predation and the energy drain on the female who must often renest.

TABLE 1

Incubation Periods Determined in Captives

11 days	12 days
11 days	12 days
11 days, 6 hours	12 days
11 days, 7 hours	12 days*
11 days, 9 hours	12 days*
11 days, 12 hours	

TABLE 2

Age at Fledging in Days

Age	Number of nestings	
	Z. leucophrys (Blanchard **, 1941)	*Z. capensis*
8 days	1	0
9	0	0
10	8	2
11	3	3
12	0	3
average	10.1	11.1

* In these instances we cannot rule out the possibility of the period being 11 days and about 9 to 12 hours.

** Blanchard (Oakeson, 1954) later reported records for fledging of three races of *leucophrys;* these are presented on an individual rather than nest history basis and with means and extremes only which make comparison with *capensis* difficult. However, her further records, while suggesting some latitudinal and racial differences, further confirm fledging averages for the species *leucophrys* that are a day or more less than for *capensis.*

TABLE 3

Pair Association through the Year

Pairs			
Male	Female	Actual observed association	Number of known breeding seasons involved
466	485	February to January	3
468	471	June to December	2
482	483	April to January	2
484	478	May to December	2
495	494	July to January	2
496	477	July to January	2
805	498	July to January	2

TABLE 4

Sample Records of Start of Dawn Singing

February	17	5:55
February	18	5:55
April	9	5:56
April	13 (clear)	5:36
May	10	5:30
June	25 (clear)	5:28
September	20	5:38
December	8	5:33
December	18	5:37

TABLE 5

Survival of Birds Banded in Early 1958

Adults and birds 6 months or more old engaging in first nesting

Initial banding		Months of survival										Survival for entire year (11 + months)
Feb. 10 - Mar. 2		0	1	2	3	4	5	6	7	8	9	
Males	15			1	1				1			12
Females	16		1		1	1		1	1		1	10
Totals	31		1	1	2	1		1	2		1	22

Juveniles and birds in postjuvenal molt

												Survival for entire year (10 - 11 months)
Feb. 14 - Mar. 15		0	1	2	3	4	5	6	7	8	9	
Totals	30	9	7	4	1	1			1	1	2	4
									(♀)	(♀?)	(♂,♀)	(all ♂♂)

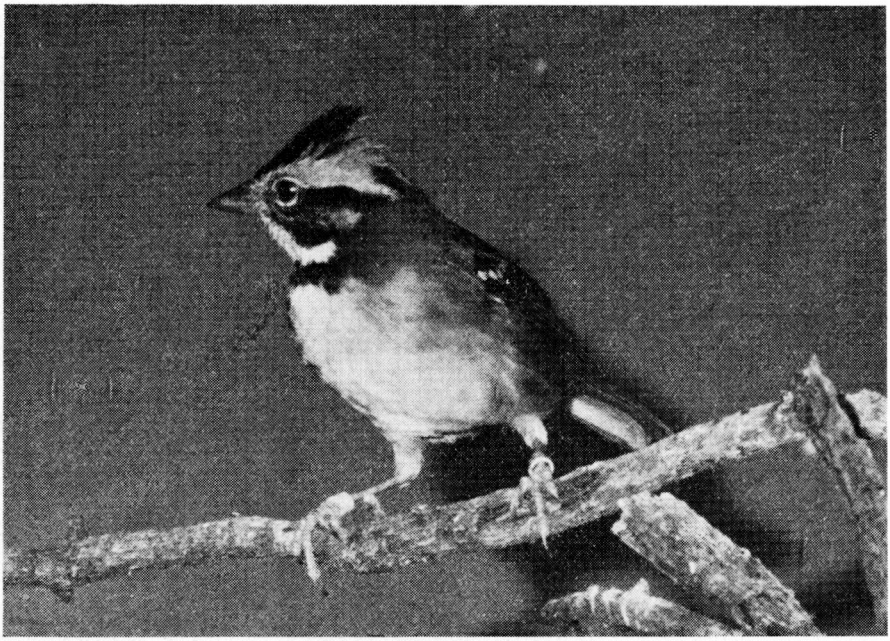


PLATE 1 a

Adult Andean sparrow, *Zonotrichia capensis*, in captivity, showing alert posture with crest elevated.

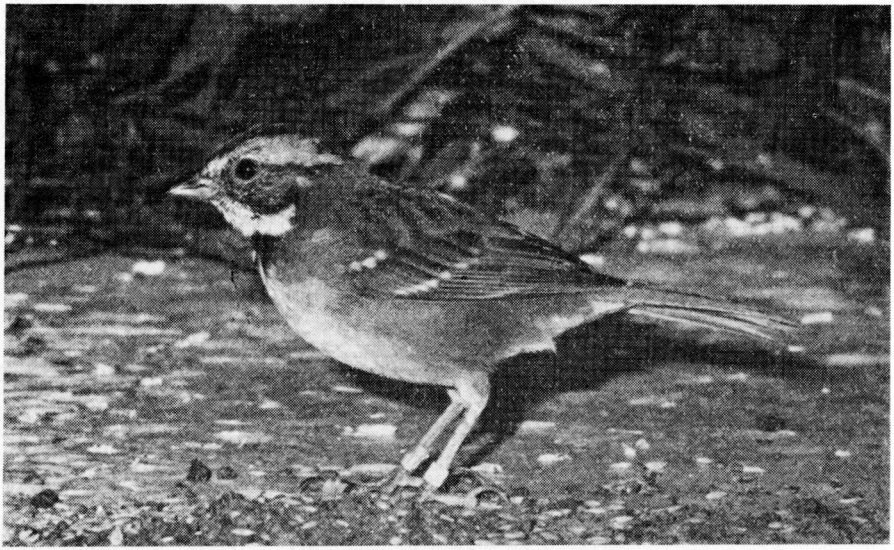
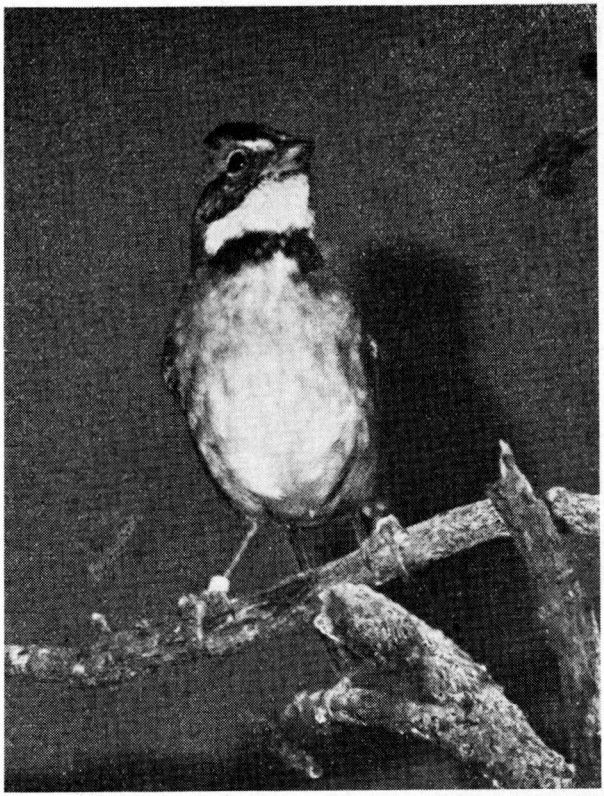


PLATE 1 b

Adult on ground, foraging, with the head profile rounded owing to depression of the crest.



a.

b.

PLATE 2

a. Adult *Zonotrichia capensis* in erect posture of alertness and aggressiveness. By drooping the wings and fanning the tail, the bird would change from this to the strutting pose. *b.* An Andean sparrow at left, in horizontal crouching threat posture with bill open in preparation for jabbing.

PLATE 4 a

A nest site on the ground, March 7, 1965, 8 kilometers northwest of San Antonio.

PLATE 4 b

Nest and eggs of *Zonotrichia capensis* situated in a small bush near the Santo Domingo station. Photograph by F. C. Carlos Lehmann V.

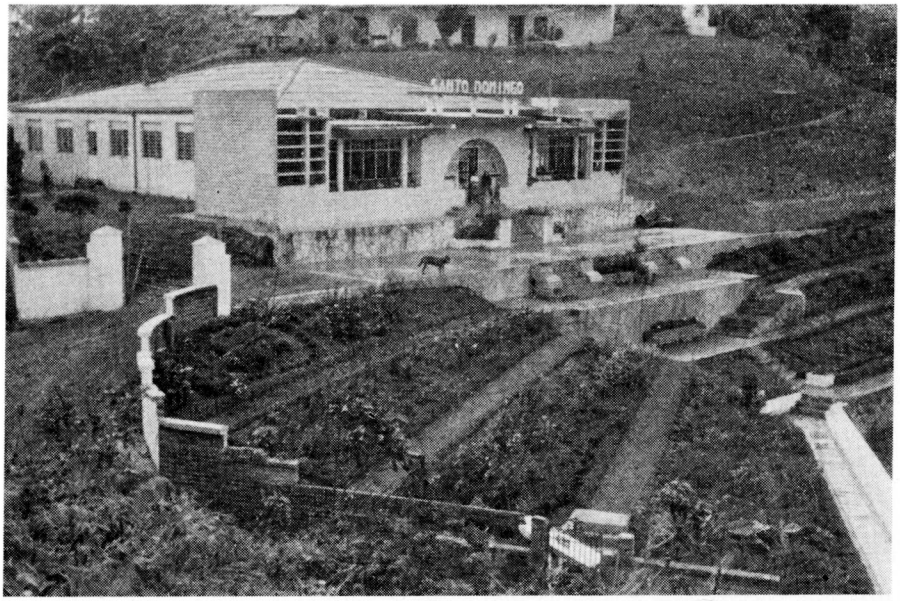


PLATE 3 a

The station at Santo Domingo, 4 kilometers northwest of San Antonio, 6500 feet elevation, in the Western Andes, Valle, Colombia. The principal study of territories and of field behavior in 1958 was conducted in the gardens and pastures about the house. Photograph by F. Carlos Lehmann V.

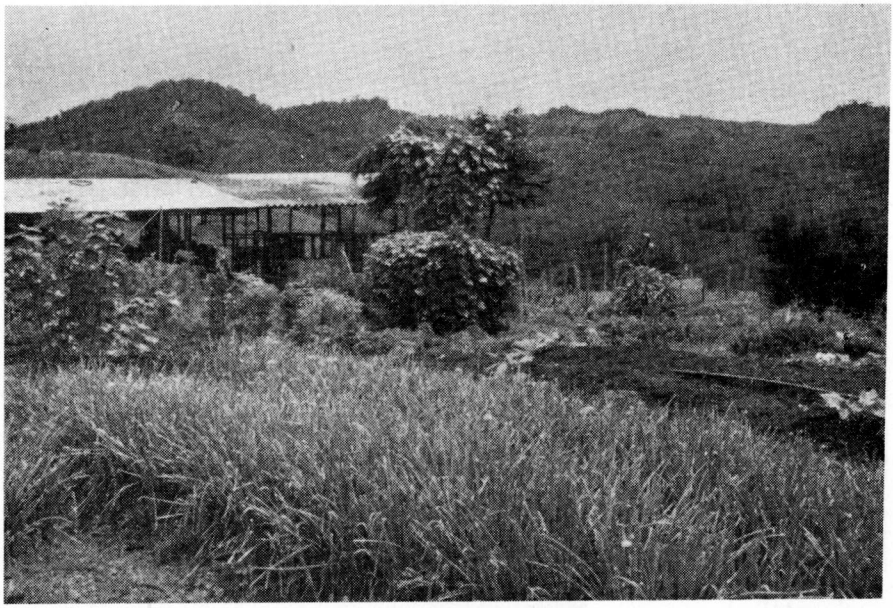


PLATE 3 b

Garden habitat and feeding areas of *Zonotrichia capensis* in March of 1965, 8 kilometers northwest of San Antonio, 6500 feet.

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